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BY

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By Walter Kenrick Fisher

The echiuroids, sometimes called spoon worms from the shape of the contracted prostomium or proboscis, are cigar-shaped or sausage-shaped creatures, essentially highly muscular sacs filled with fluid in which the long alimentary canal and other organs have great freedom of movement. The mouth is anterior, usually at the base of a snout or a long proboscis used for gathering food. The skin is highly glandular and is covered by a very thin cuticle. Typically there are two hooked setae behind the mouth, and two genera have either one or two circles of setae at the posterior end of the body. The alimentary canal, in contrast to that of most annelids, is several times the length of body and consists of a long foregut, differentiated into pharynx, esophagus, gizzard, and stomach, a still longer midgut or intestine, accompanied for a considerable part of its length by a collateral intestine, or siphon, and finally a short hind-gut or cloaca, into which empty two usually voluminous, sometimes branched, vesicles, the walls of which are studded with minute ciliated funnels. The anterior nephridia, typically elongate, thin-walled sacs, varying from one to many, but usually from one to four pairs, have a basal or terminal nephrostome, the lips of which may be greatly prolonged and spirally twisted. The nephridia vary greatly in size and when filled with eggs or sperm are often very large. The vascular system consists of a ventral vessel following the nerve cord to form a loop in the proboscis from the tip of which a median vessel passes backward in the proboscis and along the dorsal side of foregut to beginning of midgut, where a neurointestinal vessel joins it to the ventral vessel. In *Urechis* there are no blood vessels.

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Echiuroids are burrowers in mud or sand, where they fashion more or less permanent tunnels. Sometimes they live under rocks; sometimes in mud-filled mollusk shells or sand-dollar tests, which afford some protection; or they inhabit the rock galleries excavated by boring clams. Their food consists of organic material contained in the mud which they swallow in large quantities, or of lighter organic detritus selected by the usually long proboscis. In the same species from different localities the intestinal pellets vary with the character of the bottom. One genus (*Urechis*) has very specialized feeding habits and uses only finely divided material, including bacteria. It is probable that any small organisms living in the surface film of mud will be eaten by echiuroids. Gislén (1940, p. 30) found the intestinal pellets of *Echiurus echiurus* "to consist of the same stuff as that which is formed by the detritus-film growing on the aquarium bottom. There are thus plenty of sand grains; further the pellets consist of diatoms, algal threads, debris of leaves of phanerogams (*Zostera* et al.), Infusoria, Bacteria, occasional Nematodes and Rotatoria and, to a large extent, of amorphous brown stuff which emanates from decomposed organic substance."

The smallest sexually mature echiuroid I have ever seen is a *Listriolobus pelodes* 7 mm. long (0.275 of an inch), and the largest is *Urechis caupo*, 470 mm. long preserved, or 18.5 inches. I have seen a relaxed living *Urechis caupo* 19.75 inches long. The Japanese *Ikeda taenioides*, a remarkable and isolated form, attains a body length of 16 inches with a proboscis of 58 inches, or a total length of 6 feet 2 inches (Ikeda, 1907, p. 20).

More helpless, unprotected animals can scarcely be imagined. The immature stages are prey for every predaceous inhabitant of the sea bottom. The adults are regularly eaten by fishes, especially flatfishes and rays, as well as by the Indians of Chiloé Island, Chile (Gay, 1854, p. 475). In Japan and Korea *Urechis unicinctus* is extensively used as bait. Sato (1939, p. 319) states that in Korea the natives catch it by means of iron hooks and dry it for food.

Systematics of the Echiuroidea present the usual problems in addition to others inherent to the group. The principal difficulty is the lack of structures having a permanent form. The setae are of very limited use; everything else is soft and capable of distortion. The practical difficulties encountered are those which would confront the student of holothurians if these creatures did not carry embedded in the skin a species label in the guise of characteristic calcareous deposits. Most of the generic and specific characters of echiuroids must be sought by careful dissection of the internal organs, which are susceptible to variation arising from accidents of fixation. Nevertheless, a fairly satisfactory system of genera can be constructed. But it is obvious that closely related species may not be recognized,

or if recognized they may be impossible to describe in the absence of trenchant characters. Descriptions of echiuroids based on external characters or on a very summary enumeration of a few internal features have made it difficult to determine the generic position of a number of described forms.

It has been a time-honored procedure to classify the echiuroids, sometimes in combination with the sipunculoids and priapuloids, under the name Gephyrea, as a class of the Annelida. In 1898 Prof. Adam Sedgwick, in his "Students' Textbook of Zoology," set up separate phyla for the Sipunculoidea and Priapuloidea but retained the Echiuroidea as a class of the Annelida. Since the development of *Urechis caupo* has been thoroughly elucidated (Newby, 1940), it is now known that the echiuroids are not more closely related to annelids than to mollusks. Dr. Newby writes at length on a comparison of echiuroid development with that of the other invertebrates and on the phylogenetic position of the Echiuroidea. In conclusion he says (p. 209):

> There are many echiuroid characteristics which indicate that this group is separate from the annelids: (a) The mode of development of the first somatoblast is different. (b) The anus is not homologous in the two groups and no proctodaeum is formed in echiuroids. (c) The mesodermal bands do not develop teloblastically in echiuroids. (d) The elongation of the larva is not teloblastic in echiuroids. (e) Three layers of body muscles are formed in echiuroids. (f) The ectomesoderm contributes to the body musculature in echiuroids. (g) A ciliated intestinal groove is formed in echiuroids and this becomes the primordium of the siphon. These structures are not found in the annelids. (h) Anal vesicles, probably of endodermal origin, are found in echiuroids. (i) The coecum of the larval digestive tract becomes a linear part of the adult tract in echiuroids. (j) The mesodermal bands of echiuroids show no evidence of segmentation. (k) The lack of segmentation in the mesoderm considered with the questionable nature of the segmentation of the nervous system and mucous glands and further considered with the "segmentation" of the shell glands of the chitons (molluscs) makes it appear probable that the echiuroids have a primary lack of metamerism.
>
> Against these numerous differences there are only three clear-cut characteristics in common between the echiuroids and annelids which are not also possessed by the mollusks. (a) The annelidan cross develops in both groups. (b) Both groups possess setae. (However setae are to be found in another group of animals [Brachiopoda] which do not belong to the Annelida.) (c) The lateral halves of the nervous system become merged into single, unpaired structures.
>
> With the above facts in mind it is evident that the echiuroids are only distantly related to the annelids. When numerous differences which appear in their development are considered, it seems improbable that the inclusion of the echiuroids with the annelids as a sub-phylum or class, is justified. It is probably more accurate to consider the Echiuroidea as forming a separate phylum, distinct from the phylum Annelida, and I herewith propose that they be so considered.

In the keys no mention is made of *Epithetosoma* Danielssen and Koren, 1881. Théel (1906, p. 9) has demonstrated satisfactorily that the animal is not an echiuroid, but most likely a nemertean.

Neither is *Poeobius meseres* Heath (1930) included. This remarkable pelagic transparent worm was first taken in 350 meters, Monterey Bay, Calif., and was later found to be abundant off southern Alaska. Its anatomy has been fully described by Professor Heath. Subsequently the writer observed and sketched a living animal. The blood vessels are clearly visible and contain a dull green fluid, but the enlargement of the dorsal vessel is dull red. Blood vessels extend to tip of the 2 prostomial palps and the 10 (possibly peristomial) cirri.

The creature has no paired appendages, no somatic segmentation, and no setae. "The nervous system conforms to the usual annelidan type, with supra-oesophageal ganglion, circum-oesophageal connectives, and a ventral nerve chain comprising 11 pairs of ganglia with the usual commissures and connectives. The somatic musculature comprises four great longitudinal bands, extending throughout the length of the body, and a more delicate external sheath of circular fibres." This is the annelid pattern and distinctly not the echiuroid. The head is unlike that of any known echiuroid but resembles that of some polychaete annelids. The alimentary canal and nephridia seem to the writer to be specialized in much the same way as in the case of *Sternaspis*, which in one species (*S. spinosus* Sluiter) has the prostomium prolonged outward on each side to form a grooved palplike organ. The Scoleciformia, however, have definite mesodermal segmentation.

The difficulty in finding a place for *Poeobius* may well mean that it is not an annelid or a echiuroid or a link between the two. Although nothing whatever is known of the development of *Poeobius*, we have to assume that mesodermal segmentation is absent; therefore it is not an annelid. Its nerve cord is segmented (implying pseudometamerism). The nerve cord of larval echiuroids is segmented, but this is lost in the adult, suggesting that the ancestors, while deprived of mesodermal metamerism, still had a pseudometamerism of the nerve cord. A tenable hypothesis is that the echiuroids and *Poeobius* stemmed from a common group that was as fundamentally unsegmented as the Amphineura among mollusks. According to this view *Poeobius* is the survivor of a lesser phylum, comparable to the Phoronidea and Priapuloidea. As the genus now floats in a sort of taxonomic limbo, it may be provisionally assigned to a new phylum, POEOBIOIDEA.

The region covered by this report includes all the water north of a line drawn from Cape San Lucas, Baja California, to the southern end of Sakhalin Island on the east Asiatic coast. The Gulf of California has been included, and a species long ago dredged by the *Albatross* in Japanese waters has been added, as it modifies the concept of *Acanthohamingia*, which I wished to include in the key.

The specimens upon which this paper is based have been accumulated slowly over a considerable period of years.[1] In addition, the material belonging to the United States National Museum was placed at my disposal, and an important collection belonging to the Allan Hancock Foundation of the University of Southern California was tendered by Dr. Olga Hartman. The types of all the new species are in the collection of the National Museum.

The following new genus, based on an extralimital species, will be found in the text: *Lissomyema*, type *Thalassema mellita* Conn (under *Listriolobus*).

Phylum ECHIUROIDEA[2]

Echiuroidea SEDGWICK, 1898, p. 527 (class of Annelida).

Unsegmented, bilateral, fusiform or sacculiform animals with anterior mouth and posterior anus, but no proctodaeum; a long convoluted alimentary canal lying in a spacious coelom of schizocoelous type; a muscular body wall composed of three layers, of which the middle (with one exception) is composed of longitudinal fibers; with one to very numerous anterior nephridia functioning as gonothecae; with typically two anal vesicles having numerous ciliated funnels and functioning as excretory organs; alimentary canal typically with collateral intestine or siphon; usually with a prostomial proboscis, which may exceed length of body but which is sometimes absent; usually with ectodermal setae, of which two, ventrally situated behind mouth, are most constantly present, together with sometimes one or two circles at posterior end of body; but setae absent in a few genera; ventral nerve cord unsegmented forming, around the mouth, a loop which follows border of proboscis; gonad, where known, in mesentery above nerve cord, or in the mesenteries surrounding cloaca.

KEY TO CLASSES

a[1]. Body wall with innermost circular or oblique layer of muscles well developed; anal vesicles present; collateral intestine or siphon well developed; proboscis and anterior setae present in nearly all species---**Echiurida** (p. 220)

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[1] I am especially beholden to my former colleague Prof. George E. MacGinitie for material of *Urechis caupo*, *Listriolobus pelodes*, and *Ochetostoma octomyotum;* to Edward F. Ricketts for the type of *Echiurus echiurus alaskanus* and a small collection made by him and John Steinbeck in the Gulf of California; to Dr. Olga Hartman for a specimen of *Lissomyema mellita;* to Prof. S. F. Light for a perfect specimen of *Listriolobus pelodes;* to the Museum of Comparative Zoology for a specimen of *Urechis chilensis;* to Dr. W. L. Lloyd, Cabrillo Marine Museum, San Pedro, Calif., for the loan of a specimen of *Ochetostoma octomyotum;* to Prof. John H. Gerould for the loan of several rare reprints; and to Dr. Waldo L. Schmitt, U. S. National Museum, for numerous favors.

[2] Echiuroidea was introduced as a subphylum by A. H. Clark (Bull. Inst. Océanogr. Monaco, No. 400, p. 24, 1921) and as a phylum by W. W. Newby (1940, p. 210) and Libbie H. Hyman (1940, pp. 34, 58). As a matter of record, Edward F. Ricketts was the first to use Echiuroidea as a phylum name, in an excellent semipopular text "Between Pacific Tides" (Ricketts and Calvin, 1939, p. 272), perhaps incited thereto by the present writer who has advocated this procedure to his classes for 20 years.

a^2. Body wall with innermost circular layer missing or degenerated to a net of fibers; no anal vesicles; apparently no siphon; no proboscis and no setae ---------- **Sactosomatida**[3]

Class ECHIURIDA

KEY TO ORDERS

a^1. In body wall longitudinal muscle layer lying between outer circular layer and inner oblique layer; nephridia, normally paired, not excessively numerous.

b^1. A closed blood-vascular system; no specialization of intestine for anal respiration ---------- **Echiuroinea** Bock (p. 220)

b^2. No vascular system, coelomic fluid being heavily charged with large blood corpuscles containing hemoglobin or hemoglobin plus hematin; intestine with terminal portion enlarged, thin-walled, to receive water from cloacal pump ---------- **Xenopneusta**, new order (p. 262)

a^2. Longitudinal layer of body wall lying outside of both the circular layer and inner oblique layer; nephridia excessively numerous, unpaired (and with terminal nephrostome); proboscis excessively long.

Heteromyota,[4] new order

Order ECHIUROINEA Bock, emended

A closed blood-vascular system; no specialization of intestine for anal respiration.

KEY TO FAMILIES

a^1. Dimorphic; male degenerate, planarianlike, parasitic in or on female; female resembling *Thalassema* but with bifid proboscis in some genera; anal vesicles consisting of branched tubules ending in numerous ciliated cups; anterior setae sometimes present; posterior setae absent ---------- **Bonelliidae** (p. 249)

a^2. Not dimorphic; proboscis usually conspicuous, sometimes several times length of body, but never bifid; absent in one genus; anal vesicles not branched but in form of elongate sacs, surface of which is covered with minute cilated funnels; anterior paired setae present in all genera, posterior setae in *Echiurus* only ---------- **Echiuridae** (p. 221)

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[3] New name for Saccosomatida Théel (1906, p. 14). Théel instituted the group as a suborder for *Saccosoma vitreum* Danielssen and Koren (1881, p. 34, pl. 6, figs. 1–8). This species is based on a single small example dredged in 1,215 fathoms north of the Faroe Islands. It is a female and the species may prove to be dimorphic, as there is a single nephridium filled with eggs and opening near the mouth. The proboscis may have been lost. It is aberrant from all other echiuroids and may not be an echiuroid. *Saccosoma* Danielssen and Koren is preoccupied by *Saccosoma* Motschoulsky, 1859, in Coleoptera (Bull. Acad. St. Pétersbourg, vol. 1, column 304). The new name "Sactosoma" (with identical meaning) is proposed to replace *Saccosoma* Danielssen and Koren.

[4] Based on the remarkable genus *Ikeda* Wharton, 1913, pp. 243–270. Type, *Thalassema taenioides* Ikeda, 1904, p. 63; 1907, p. 16, pl. 1, fig. 3; pl. 2, figs. 18–22; pl. 3, figs 23–36; pl. 4, figs. 37–47. This large echiuroid, with a proboscis upward of a meter or more in length and nephridia from 200 to 400 in number without indication of paired arrangement, is so different from the general run of the phylum that it deserves to be set apart as the type of at least a distinct order. The arrangement of muscle layers is different from that of all other echiuroids and indicates a long separation from typical stock. See Sato, 1931. p. 179.

Family ECHIURIDAE (de Blainville, 1827, restricted)

KEY TO GENERA

a^1. Two circles of posterior setae..... **Echiurus** Guérin-Méneville (p. 225)
a^2. No posterior setae present.
  b^1. Proboscis absent..... **Arhynchite** Sato (p. 247)
  b^1. Proboscis present.
    c^1. No differentiated thicker bands in longitudinal muscle layer.
      d^1. Nephrostome of nephridia without elongated, spirally coiled lips. **Thalassema** Lamarck (p. 230)
      d^2. Nephrostome with elongated, spirally coiled lips. **Anelassorhynchus** Annandale (p. 221)
    c^2. Longitudinal muscle layer with very slight to pronounced differentiation into longitudinal bands, 8 or more in number.
      d^1. Nephrostome of nephridia without spirally coiled lips; inner layer of muscles not differentiated into separate transverse fascicles between longitudinal bands..... **Lissomyema**, new genus (p. 224)
      d^2. Nephrostome with elongated spiral lips.
        e^1. Differentiated longitudinal muscle bands weak, zones between not showing a fasciculate arrangement of inner oblique muscles; in small specimens longitudinal bands very faint or visible only in posterior region..... **Listriolobus** W. Fischer (p. 233)
        e^2. Longitudinal muscle bands strongly developed, zones between crossed by separated fascicles of innermost, oblique layer.
          f^1. Nephridia in 1 to 5 pairs; vascular ring vessel at beginning of midgut..... **Ochetostoma** Leuckart and Rüppell (p. 240)
          f^2. Nephridia, at least in male, in 6 to 14 groups of 1 to 4, the groups arranged in pairs; vascular ring vessel at posterior end of pharynx..... **Ikedosoma** Bock (p. 224)

Remarks.—In the foregoing synopsis all the generic divisions, with the exception of *Echiurus*, are the result of subdividing the old genus *Thalassema*. In a very real sense these groups are provisional because adequate descriptions and figures of the internal structure of many species have not been published.

THALASSEMA Lamarck.—The genus has been restricted to a few species grouped around the type, *Thalassema thalassema* (Pallas), generally known as *Th. neptuni* Gaertner. The middle, longitudinal layer of muscle fibers of body wall shows no sign of differentiation into thicker bands. The internal opening of the nephridia is very simple, without prolongation into spirally coiled lips.

ANELASSORHYNCHUS Annandale (1922, p. 148).—It may not be of any practical value to recognize this group. The species differ from *Thalassema* in having the nephrostome lips prolonged and spirally coiled, but little is known of other details of the internal anatomy. Annandale based the genus on the structure of the proboscis of four estuarine species occurring in brackish water of India and Siam. He says:

> The genus consists of Echiuridae allied to *Thalassema* Gaertner, but differing in the structure, function, and physiology of the proboscis. This organ is relatively stout and short, incapable of great prolongation or autotomy. The ciliated

groove on its ventral surface is feebly developed and the lateral margins of the ventral surface bear (except in *A. microrhynchus*) gill-like outgrowths. The longitudinal muscle-fibres of the body form a single sheath and the musculature bears a close resemblance to that of some species of *Thalassema*. There are two pairs of nephridia. The anal funnels are simple and thin-walled; their ciliated funnels are minute.

The type-species is *A. branchiorhynchus* (Annandale & Kemp). The other species are *A. dendrorhynchus* (Annandale & Kemp), *A. sabinum* (Lanchester) and *A. microrhynchus* (Prashad).

It seems to me that the modifications of the proboscis, which exhibit a number of gradations in complexity, are adaptations to an ecology in various ways abnormal, a parallel development being found in *Ochetostoma arkati* (Prashad). But these species agree with certain others in having a more specialized nephrostome than is found in *Thalassema thalassema* and close allies.

1. With two pairs of nephridia (behind the setae): *sabinum* Lanchester, *branchiorhynchus* Annandale and Kemp, *dendrorhynchus* Annandale and Kemp, *microrhynchus* Prashad, *semoni* Fischer.

2. With three pairs of nephridia, all three opening behind the setae: *mucosa* Ikeda, *vegrande* Lampert (no proboscis). First pair opening in front of setae: *inanense* Ikeda, *moebii* Greef.

Unless some definite character other than the nephrostome is discovered, there will be a practical difficulty in distinguishing young *Listriolobus*, in which the differentiation of longitudinal muscle bands is very weak.

Lissomyema.—Through the kindness of Dr. Olga Hartman I have received a specimen of *Thalassema mellita* Conn collected by her at the type locality, Beaufort, N. C., in June 1940. It is 36 mm. in length, with proboscis 16 mm. additional. From the outside the eight longitudinal muscle bands are clearly visible. Figure 10 represents a dissection of the anterior portion. The muscle bands are much more sharply delimited than in *Listriolobus* by having an incipient fasciculation of the muscles of the oblique layer, possibly representing the first stage in the differentiation of the strong transverse bundles characteristic of *Ochetostoma*. The species has simple fan-shaped nephrostomes and very heavy interbasal and radiating seta muscles. The gizzard is relatively short and the stomach (*C*) is relatively long. An individual variation is the presence of three nephridia on one side and two on the other. The species is described

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Figure 10.—*Lissomyema mellita* (Conn): Dissection of anterior region of a specimen from Beaufort, N. C., × 12. Six of the eight muscle bands are diagrammatically indicated by dots. The alimentary canal is drawn to the right to disclose the organs beneath it. (B^1, B^3, B^4, dorsal, neurointestinal, and ventral blood vessels; *C*, stomach; *G*, gizzard; *I*, intestine; *MD*, middorsal muscle band; *MI*, interbasal muscle; *MV*, midventral muscle band; *N*, nephridia; *NC*, nerve cord; *O*, esophagus; *P*, pharynx; *S*, seta; *Si1*, beginning of siphon.)

FIGURE 10.—(See opposite page for legend).

as having two pairs. The anal vesicles are voluminous with numerous conspicuous ciliated funnels. The ventral blood vessel sends an important branch to the pharynx and esophagus.

For this species, therefore, I propose the new genus **Lissomyema,** which differs from *Thalassema* in having eight well-differentiated longitudinal muscle bands and incipient fasciculation of the oblique layer; from *Listriolobus* and *Ochetostoma* in having simple fan-shaped nephrostome without trace of spiral extensions. Type, *Thalassema mellita* Conn. (Fig. 10.)

IKEDOSOMA Bock.—*Thalassema elegans* Ikeda[5] does not belong in *Thalassema*. Ikeda (1907, p. 50) writes: "All the longitudinal lines visible on the outside, excepting the one which runs in the mid-ventral line and is superposed by the nerve-cord, appear on the inner surface of the body-wall as slightly elevated *narrow ridges or thickenings of the longitudinal muscular layer*. In the ten zones separated from one another by the above lines, the circular muscle fibres form more or less regularly arranged transverse bundles." This structure of the body wall closely approximates that of *Ochetostoma*, but *elegans* is peculiar in having numerous (13 to 27) nephridia in six or seven pairs of groups comprising one to three nephridia each. "The internal opening present at base is provided with 2 relatively short spiral lobes." The dorsal blood vessel ends with the "heart" on the hind end of the pharynx and is therefore shorter than in typical Echiuridae. "The neuro-intestinal vessel arises from the ventral median point of the ring-sinus, which surrounds the extreme hind end of pharynx" (*ibid.*, p. 52). There is no interbasal muscle and no intestinal coecum.

Thalassema gogoshimense Ikeda (1904, p. 66, pl. 1, fig. 19) is apparently congeneric with *elegans*. The excellent colored figure shows the same white longitudinal stripes as *elegans*, reflecting the muscular structure of body wall. Ikeda says: "It shows an essential agreement with *Thalassema elegans*. Indeed, the agreement may be said to be complete, the only difference being that all the visceral organs in the present species are developed on a smaller scale in proportion to the smaller size of its body." In the females, however, the nephridia are present in *three pairs* all situated behind the setae, while in the male they are in six to eight groups, arranged in pairs, each group with one to four nephridia, which are like those of *elegans* in structure.

The above paragraphs were written and a name was assigned to the genus before I saw Bock's paper. They are retained since we independently arrived at the same conclusion.

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[5] Ikeda, 1904, p. 65; 1907, p. 47, pl. 1, fig. 4; pl. 4, figs. 48, 49; Sato, 1939, p. 356; Bock, 1942, p. 18.

Genus ECHIURUS Guérin-Méneville

Echiurus Guérin-Méneville, 1831, p. 9, pl. 6, fig. 3 (ex Shipley, 1899, p. 342) (type, *Lumbricus echiurus* Pallas, 1766 = *Echiurus pallasii* Guérin-Méneville, 1831).—Skorikov, 1909, p. 80.—Spengel, 1912b, p. 173.

Echiuridae with two rings of posterior bristles, a well-developed proboscis, two or four nephridia (without spirally coiled lips), and a postpharyngeal diaphragm, which separates incompletely the small head coelom from the perivisceral cavity.

ECHIURUS ECHIURUS ALASKANUS, new subspecies

Plate 20

Echiurus Pallasii C. B. Wilson, 1900, p. 174.
Echiurus echiurus Spengel, 1912b, p. 183.

Diagnosis.—Differing from typical *E. echiurus* (Pallas) of the north Atlantic and neighboring Arctic Ocean in having the proboscis strongly attached to the body and in having the posterior setae definitely curved rather than nearly straight. Length of type, 230 mm. plus much contracted proboscis, 20 mm.

Description.—Length of body upward of 230 mm., commonly 100 mm., stout; proboscis adherent, fleshy, convex above, the edge incurved ventrally, subtruncate distally, usually 15 to 20 mm. long in contracted state. On ventral surface of the proboscis a differentiated thickening extends as a low ridge from the mouth for about one-fourth length of proboscis but sometimes considerably farther. The integument is roughened by rings of prominent verrucae most crowded at ends of body. In the middle region, where they are generally less crowded, rings of more prominent verrucae alternate with zones of three to five rings in which the verrucae are smaller or more widely spaced, or both. The appearance depends largely upon the degree of contraction of the body muscles.

The anterior setae are stout, strongly curved, and situated back of the base of proboscis a distance equal to about its greatest width. In each circle of anal bristles there may be variations of 6 to 8, as: 8–8 (posterior ring); 8–7; 8–6; 7–7; 7–6. In some specimens where the number is less, inequality of spacing indicates loss of setae. These posterior setae vary in degree of curvature but are slightly more curved than in typical *E. echiurus*. The anterior setae have a strong interbasal muscle connecting their inner ends. Occasionally a second seta, in process of formation, accompanies one of the primary. The principal posterior muscle from the setae attaches to body wall just behind the anterior nephridium.

The inner circular layer of body muscle shows a division into closely placed fascicles at each end of body, where the animal is normally most contracted.

Nephridia 4, the anterior pair close behind the setae and a little farther from nerve cord. The funnel is conspicuous, with an undulating or frilled border, but is not prolonged into spiral lips. The nephridia of all specimens examined (taken in summer months) were contracted. In some cases they were very small, and the anterior pair very inconspicuous.

Anal vesicles are simple, elongate, thin-walled sacs attached to ventrolateral wall of the cloaca and closely beset with minute ciliated funnels.

Diaphragm (pl. 20, figs. 1, 4). The diaphragm is a curious, thin-walled, funnel-shaped septum incompletely separating the peripharyngeal coelom from the general body cavity. Its general form is best appreciated from the figure in which it is shown in a semidiagrammatic fashion. The anterior, roughly circular edge is completely attached to the body wall, while ventrally it is attached to body wall on each side of the nerve cord (which here lies within the ventral mesentery of pharynx and esophagus). A large oblique posterodorsal opening of the diaphragm (with complete free edge) allows the esophagus (with its strong ventral mesentery) to pass backward into the general coelom, sometimes above and sometimes below the interbasal muscle. The rim of aperture apparently has a sphincter. The two halves of the double ventral mesentery of esophagus merge with diaphragm along its paraneural part and a short distance above the nerve (pl. 20, fig. 5).

Alimentary canal. The pharynx remains always in the peripharyngeal coelom. It is attached to the body wall by numerous strong muscular strands having an annular arrangement. There is a continuation forward of the double ventral and dorsal mesenteries separated into frenula. The dorsal blood vessel lies in this mesenterial complex. The head cavity is therefore much occluded by tissue. The lining of pharynx is anteriorly thrown into coarse folds.

The esophagus begins just behind the region of the radiating frenula of pharynx. It has, in the anterior portion, a dorsal mesentery of slender separate strands, but there is a double membranous ventral mesentery throughout its whole extent. This mesentery is anchored in the peripharyngeal chamber on each side of the nerve cord, where, a short distance above body wall, it merges with the diaphragm. By means of its muscular mesenteries, all of the esophagus can be withdrawn into the head cavity.

The esophagus, on passing *through* the right side of the diaphragm close to posterior border, becomes a long gizzard, marked by rings, which are prominent annular ridges of the lining. Beginning with the gizzard the alimentary canal is moored only by dorsal mesenterial ribbons as far as the cloaca, which has radiating muscular frenula. Along the dorsal side of the gizzard held by a perforated mesentery

is the voluminous dorsal blood vessel with numerous papilliform branches, at least anteriorly.

A very short rudimentary stomach or crop lies between the gizzard and beginning of intestine (indicated by the ventral ciliated groove). The lining of stomach is thrown into 12 strong longitudinal folds, contrasting sharply with the annular folds of gizzard. Where the stomach becomes intestine, the dorsal blood vessel splits to form the ring vessel.

The intestine has the usual three parts: presiphonal, siphonal, and postsiphonal. The first is about as long as the gizzard, or a little longer if relaxed.

The siphonal part, roughly 20 to 25 times length of presiphonal part, is marked by longitudinal folds of the lining which are evident superficially. The siphon is about one-fourth the diameter of the intestines.

The postsiphonal intestine has thinner walls and is about 10 times the length of presiphonal segment. The ciliated groove forms a ridge along its ventral side, and ends at a coecum (not always inflated) just in front of the cloaca. The fecal pellets which fill this part of the intestine are elongate ellipsoids and sometimes contain coarse material. I have found leaves of the hemlock (*Tsuga*).

Vascular system. This consists of a dorsal and ventral blood vessel and neurointestinal connective. These vary in caliber in different specimens. The dorsal vessel is likely to be considerably inflated over part or the entire length of gizzard, with irregular lobose swellings anteriorly. The ventral vessel, attached to middorsal line of nerve cord, ends posteriorly as a solid cord just in front of the intestinal coecum. The neurointestinal connective results from the branching of the dorsal vessel at the beginning of intestine by which the neurointestinal ring (B^2) is formed. The connective branches again (B^3), to form the muscle ring, before merging broadly with the ventral vessel (B^4).

Type.—U.S.N.M. No. 20609.

Type locality.—Auk Bay, Juneau, Alaska, collected by E. F. Ricketts, August 14, 1931.

Specimens examined.—One hundred and twenty-four as follows:

Collection of Stanford University

Kukak Bay, Shelikof Strait, Alaska, 12 specimens, under rocks, in mud; McMillan, 1924.

Wrangell, Alaska, 37 specimens; A. W. Greely and R. E. Snodgrass, 1897.

Auk Bay, near Juneau, Alaska, 3 specimens, slate beach, under rocks, in muddy sand, lowest intertidal zone, July 17, 1931; E. F. Ricketts (also type from this locality, August 14, 1931).

Huston Inlet, Queen Charlotte Islands, British Columbia, 42 specimens; W. F. Thompson, July 1, 1913.

Alaska, possibly Dutch Harbor, Unalaska, 5 specimens.

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Cape Smyth, Alaska, 3 fathoms, No. 850, Point Barrow Expedition; 2 specimens in very bad condition, without proboscis; possibly these are intermediate with true *echiurus*.

Off Cape Strogonof, Alaska, *Albatross* station 3291, lat. 56°58′30″ N., long. 159°11′ W., 26 fathoms, black sand, gravel, 1 specimen from stomach of cod, in poor condition.

Bristol Bay, Alaska, No. 4597, 2 specimens, one lacking proboscis.

Unalaska, Alaska, No. 16314, 2 specimens.

Bering Island, Nos. 4151, 16315, 2 specimens, typical.

Alitak Bay (head of Lazy Bay), Kodiak Island, gravelly sand, January 22, 1941, 5 specimens.

Stepovak Bay, Alaska, 15–90 fathoms, October 24, 1940, 1 specimen.

Dolgoi Harbor, Alaska, October 6, 1940, 1 specimen.

Wrangell, Alaska, No. 4538, August 28, 1882, under stones, 2 specimens.

Chasina Bay, Alaska, No. 4601, 1 specimen.

Saginaw Bay, Alaska, No. 4117, 1 specimen.

Without stated locality (probably Unalaska), 5 specimens.

Remarks.—The type specimen was taken from its burrow, a tube in sandy clay beach, 24 inches below the surface, along with a commensal polynoid annelid, *Hesperonoë adventor* (determined by Dr. Olga Hartman). The same species is commensal with *Urechis caupo*.

This, the common Alaskan *Echiurus*, differs from the typical form of Europe and the north Atlantic coast of America in having the proboscis firmly attached to the body. All writers who have handled living *Echiurus echiurus* emphasize its habit of dropping the proboscis on the slightest provocation.[6] Most of the 120 specimens of *alaskanus* were not handled with care but were simply dropped into alcohol; 106 of these specimens still have the proboscis firmly attached, while at least 5 lost the proboscis subsequent to fixing, apparently from rough handling.

Under ordinary circumstances I should have given Brandt's name *sitkaensis* to this form, assuming that Mertens would naturally have picked up at Sitka the common Alaskan species. J. W. Spengel (1912b), however, succeeded in obtaining one of Mertens's two specimens, upon which Brandt based his description, and found that it differed fundamentally from *Echiurus echiurus* in having only two nephridia, as well as in certain other respects. The name *sitkaensis* is therefore definitely associated with a type specimen which has been redescribed by one of the best zoologists of his time.

The ecology of *Echiurus echiurus* has been studied by Dr. Torsten Gislén (1940) chiefly at Kristineberg, Sweden. His very compre-

[6] Torsten Gislén says: "As stated before the proboscis is very easily thrown off. In fact probably only very few men have seen a proboscis in connection with an Echiurus. Forbes and Goodsir say that it is so slightly affixed to the body as to break off at the least touch; in only one or two cases did they find it attached, and then it broke away immediately on the removal of the animal. Only in some exceptional instances have I been able to secure specimens with the proboscis retained." (Gislén, 1940, p. 10.)

hensive memoir is in the forefront of excellence and will long serve as a model for this type of work.

ECHIURUS SITKAENSIS (Brandt)

Thalassema (*Echiurus*) *sitkaensis* Brandt, 1835, p. 62.
Echiurus sitkaensis Spengel, 1912b, pp. 184–189.

Diagnosis.—Corpus circiter tripollicare oblongum, e subbrunneo olivaceum, obscurius punctatum et transversim striatum. Proboscis latiuscula, carnea, transversim purpureo striata, apice emarginata. Unguiculi anterioris corporis partis et spiculae posterioris lutea. (Brandt.)

Differing from *E. echiurus* in having two nephridia, in lacking a differentiated ridge of tissue along ventral side of proboscis, and in having skin papillae subequal rather than in rings of larger papillae alternating with narrow zones of smaller.

Remarks.—This species constitutes one of the major mysteries in the systematics of the Echiuroidea. Mertens collected two specimens at Sitka, both of which he dissected. One of these specimens, his notes on the dissections, and a life sketch in color reached the St. Petersburg Museum and were used by Brandt. Subsequently all these became available to Spengel, as he details in his *Echiurus* paper (1912b).

Spengel made a thorough examination of what remained of the internal anatomy and was able to satisfy himself that *only two nephridia were present*, in the location of the anterior nephridia of *E. echiurus*. The proboscis was very adherent to the body, and it lacked the ridge of tissue on its concave under surface. As less important differences he lists: skin papillae subequal, in rather regular and very numerous rings (not rings of larger papillae alternating with zones of smaller); curvature of anal setae stronger than in *echiurus;* color, according to Mertens's drawing, brownish olive spotted and cross-striped with darker, the proboscis flesh color with purple transverse stripes.

The tough, nondeciduous proboscis is characteristic of the Alaskan *Echiurus* I have examined, but all these have the ventral ridge present, leaving as the principal characters of *sitkaensis* the two nephridia, absence of proboscis ridge, and the subequal papillae.

Wilson (1900, p. 174) states that he examined Alaskan specimens of *E. echiurus* (=*alaskanus*) collected by Dr. W. R. Coe in 1899. "This species was found abundantly at many different localities along the Alaskan coast south of the Peninsula and on adjacent islands, nearly always in rich black mud." I have listed 120 specimens from Alaska and British Columbia. None of these is *sitkaensis*.

If there *is* a species *sitkaensis* it may normally live below low tide and only occasionally be carried shoreward during heavy storms.

Type.—Formerly in St. Petersburg Museum; collected by H. Mertens.

Type locality.—Sitka, Alaska.

Genus THALASSEMA Lamarck

Thalassema LAMARCK, 1801, p. 328 (type, *Lumbricus thalassema* [7] Pallas, 1771, Spicilegia Zoologica, fasc. 10, p. 8, pl. 1, fig. 6).

Diagnosis.—Echiuridae with a well-developed proboscis but without anal bristles and without specialized bands in the longitudinal layer of body muscles; inner oblique layer smooth, except sometimes for a short distance at anterior end of body; anterior nephridia (gonothecae) one or two pairs, the internal ciliated funnel (nephrostome) without spiral lobes. [8]

THALASSEMA STEINBECKI, new species

FIGURE 11

Diagnosis.—Small, slightly translucent, the proboscis as long as body, broad proximally, ribbonlike distally; nephridia, two pairs, the ciliated funnel with simple subcircular opening lacking any trace of spiral lips; interbasal muscle of setae well developed, strong, passing through loop of dorsoventral blood vessel; siphon beginning a short distance from vascular ring; precloacal intestinal coecum; intestinal mesenteries including conspicuous subfusiform fleshy masses; anal vesicles as long as contracted body, covered with numerous tiny ciliated funnels. Length of body 12 mm.; of proboscis, 12 mm.

Description.—The skin is coarsely verrucose for a short distance back of proboscis and on terminal third of body; elsewhere the verrucae

[7] *Thalassema* was first used in a generic sense by Lamarck. Although Pallas (Spicilegia, 1771) mentions the name *Thalassema* as used by Joseph Gaertner, he names the animal *Lumbricus thalassema*, which appears to be the first valid binomial referring to the species generally known as *Thalassema neptuni* Gaertner. The latter is in effect a manuscript name. Neither Shipley (1899, p. 351) nor Wharton (1913, p. 265), who have offered revisions of *Thalassema*, gives any reference for the combination *Thalassema neptuni*. Quatrefages (1865, vol. 2, p. 595) cites "Thalassema Neptuni Gaertner, cité par Pallas, Spicilegia Zoologica, fasc. 10, p. 8, pl. 1, fig. 6." Forbes, 1841, in his "History of British Starfishes and Other Animals of the Class Echinodermata," gives a good account of the habits of "Gaertner's spoon-worm, *Thalassema Neptuni* Gaertner." The first item in his list of references is *Lumbricus Thalassema* Pallas.

The derivation of the word seems to be *thalassos* (sea) + *ema* (dart).

[8] Shipley (1899, p. 351) in his revision of *Thalassema* is in error in the statement that the nephridia have their internal openings spirally twisted. Lankester (1881, p. 355) writes that they are semicircular and contrasts them with the spiral sort found in *T. moebii*, as figured in Greef's "Die Echiuren" (1879, pl. 8, fig. 69).

FIGURE 11.—*Thalassema steinbecki*, new species: A, The type, × 14, showing arrangement of organs; the greater part of the intestine has been omitted and the foregut has been strongly bent to right in order to uncover the nephridia. B, A seta, × 20, from a specimen taken in 165 fathoms off San Francisquito Bay, Baja California; above, the hook, further enlarged. C, Ventral view of the type, × 4. (*AV*, Anal vesicle; B^1–B^4, dorsal, ring, neurointestinal, and ventral vessels; *C*, stomach; *CG*, ciliated furrow of intestine; *Cl*, cloaca; *G*, gizzard; *I*, intestine; *IC*, intestinal coecum; *Me*, mesenterial bodies; *MI*, interbasal muscle of setae; *N*, nephridia; *NC*, nerve cord; *O*, esophagus; *P*, pharynx; *S*, seta; *Si1*, anterior end of siphon.)

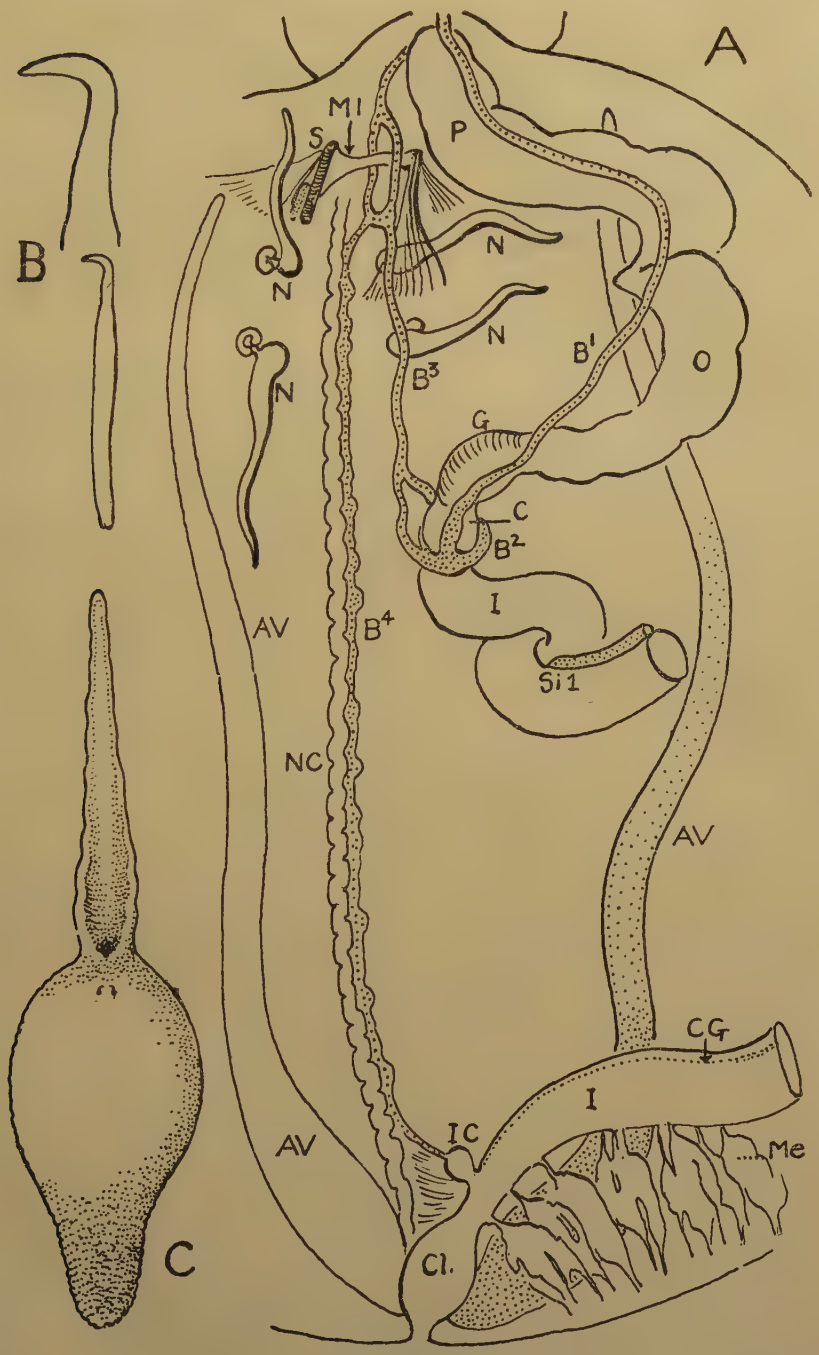

FIGURE 11.—(See opposite page for legend).

are obviously smaller, and there is a suggestion of transverse alignment. The appearance of the skin will depend a good deal on the state of contraction of body wall. The middle portion of body is slightly translucent, not transparent in places as in *Listriolobus pelodes*.

The setae have a stout interbasal muscle connecting the inner ends, from which radiate numerous fan-shaped sheets of muscle which attach broadly to the body wall. A posterior muscle passes over the first nephridium and merges with the body wall between the first and second nephridia. Setae 1.8 mm. long with a small hook, the point of which is at right angles to the shaft. In the type and a number of other specimens the hook is worn off.

Inner layer of muscles of body wall smooth except in front of anterior nephridia where there is differentiation into about a dozen bundles passing around the body. The middle layer is undifferentiated as in other species of the restricted genus *Thalassema*.

The four nephridia are small in the type, which is probably a male. In the specimen from station 2828 they are enormously inflated and full of eggs. In the type the ciliated funnel is very simple, with smooth lips forming an incomplete circle. In the female the funnel is flattened and pear-shaped and somewhat distorted by pressure, but there is no indication of elongation into spirals.

The deflated anal vesicles are as long as the body and have the appearance of being capable of inflation to a great size.

The alimentary canal is moderately long but conspicuously shorter than that of *Listriolobus pelodes*. The contents are not always formed into pellets. The foregut consists of a pharynx-esophagus, midway along which is a sharp bend. Both the gizzard and stomach are unusually short. The former is marked by ring striations. At the posterior end of the stomach is the ring blood vessel (B^2) marking the beginning of the intestine, on the lower side of which is the ciliated groove. At a distance back of the ring vessel equal to about length of gizzard and stomach the siphon begins and runs for about half length of intestine. The ciliated groove continues to the intestinal coecum in front of the cloaca. The pharynx has a conspicuous ventral mesentery, and all along the canal are numerous dorsal mesenterial strands. Posterior to the region of the siphon the mesenteries inclose, or hold, conspicuous yellowish-white masses, sometimes subfusiform or in irregular sheets, which remind one of the suet found in mammals. A squeeze reveals several sorts of cells, some of which may be immature sperm. The cloaca is small and thin-walled.

The vascular system consists of the dorsal vessel ending posteriorly in the ring vessel, from which the neurointestinal connective passes to the ventral vessel, forming a loop enclosing the interbasal muscle of setae. The ventral vessel ends posteriorly at the intestinal coecum. In the female from station 2828 the vessels are the same.

Type.—U.S.N.M. No. 20600.

Type locality.—El Mogote, near La Paz, Baja California, low tide, March 22, 1940, 1 specimen, Steinbeck and Ricketts.

Specimens examined.—Eight as follows:

Albatross station 2828, Gulf of California, 24° 11′ 30″ N., 109° 55′ W., 10 fathoms, shells, 1 specimen.

La Plata Island, Ecuador, 7–10 fathoms, rocky with nullipores, 2 specimens, Allan Hancock Foundation.

Thurloe Bay, Baja California, 8–10 fathoms, rock with gorgonids, 1 specimen, Allan Hancock Foundation.

Off San Francisquito Bay, Baja California, 165 fathoms, shale and gray mud, 1 specimen, Allan Hancock Foundation.

Ensenada de San Francisco, Baja California, 2–6 fathoms, 1 specimen, Allan Hancock Foundation.

Agua Verde Bay, Baja California, 10 fathoms, mud and coral, 1 specimen, Allan Hancock Foundation.

Dewey Channel, San Eugene Point, Mexico, 21–24 fathoms, coralline, rock, 1 specimen, Allan Hancock Foundation.

Distribution.—Baja California to Ecuador, low tide to 165 fathoms.

Remarks.—Mr. Ricketts states that the type was associated with living *Dentalium* in sandy mud a short distance below the surface. The specimen from station 2828 has the intestine filled with small fragments of shells.

As this species belongs in the restricted genus *Thalassema*, it naturally resembles *Th. thalassema*. The gizzard, stomach, and presiphonal intestine are definitely longer in the latter species and the anal vesicles smaller, although with such extensible structures it is difficult to make comparisons. It may be recorded that in alcoholic specimens there is no division of the body into three parts, which Leigh-Sharpe (1928, p. 501) reports as a characteristic of *thalassema*. The ecology of the two species is very different. Lankester (1881, p. 350) found *thalassema* on the south coast of Devonshire "in galleries excavated in the red sandstone (not limestone) which is exposed at spring tides. The galleries appear to be those formed by the Lamellibranch *Gastrochaena* which the Thalassema appropriates." Leigh-Sharpe (1928, p. 499) reports the species from borings in limestone made by the mollusk *Saxicava*, Plymouth Sound.

Named for John Steinbeck, whose expedition to the Gulf of California collected the type.

Genus LISTRIOLOBUS W. Fischer

Listriolobus Spengel, 1912c, p. 316 (*nomen nudum*).—W. Fischer, 1926a, p. 210 (no type). (Type, *Listriolobus bahamensis* Fischer.)

Diagnosis.—Differing from *Thalassema*, sensu stricto, in having elongate, spirally coiled lips to nephrostome and 8 to 16 narrow meridional thickenings of the middle, longitudinal muscle layer. Differing from *Ochetostoma* in having the inner oblique layer a smooth con-

tinuous sheet between the longitudinal bands, not divided into separate fascicles. Nephridia 2 or 3 pairs; interbasal muscle of setae present.

The character of the longitudinal muscles is not well marked in *L. pelodes* until the animal has reached a length of 15 to 20 mm. and after it is sexually mature. Apparently in *L. sorbillans* (Lampert) a similar condition exists (Wharton, 1913). Even so, the structure of the nephrostome will segregate these species from true *Thalassema*. *L. riukiuensis* (Sato, 1939, p. 359, figs. 10–13) is probably not a *Listriolobus*. There is no interbasal muscle to setae; the diagram of the blood vessels is not the *Listriolobus* pattern.

Spengel (1912c, p. 316) established *Listriolobus* for *Thalassema erythrogrammon* of Sluiter (1883) and of Wilson (1900). Sluiter's species came from Billiton in the Java Sea while Wilson's was taken in the Bahamas. Spengel had Sluiter's animal and a duplicate, from Florida, of Wilson's species, which he characterized as "nearly related." Unfortunately, as neither of these species had a valid name, *Listriolobus* was without a type and was technically a nomen nudum. Spengel did mention *Thalassema mellita* Conn as a *species inquirenda*, "which species one must include in the above genus I can not at present decide, nor even whether or not it is justifiable to include such a form as *Th. mellita*, which has bundles of longitudinal muscles that arise from thickenings of the continuous longitudinal muscle layer." A few lines farther on he says: "The animals described by Sluiter and Wilson as Thalassema should be put in the same genus with *Th. mellita* because of the nature of the sheaths surrounding the tunic muscles. I propose the generic name *Listriolobus* for the species of Sluiter and Wilson."

Wilhelm Fischer (1926a, p. 110) discusses *Listriolobus* and names Wilson's and Sluiter's species *Listriolobus bahamensis* and *L. billitonensis*. So far as I know this is the first association of *Listriolobus* with a species from which a type can be chosen. Since Fischer did not do this I will so designate *Listriolobus bahamensis* Fischer, as being the species more likely to be available for study in the future. By implication Fischer includes *Th. mellita* Conn in *Listriolobus*, but I have made it the type of a new genus, *Lissomyema*.

LISTRIOLOBUS PELODES, new species

FIGURES 12, 13; PLATE 21, FIGURES 1, 2, 4, 4a, 4b; PLATE 22

Description.—Largest specimens 40–60 mm. long and 12–25 mm. thick; proboscis capable of extension to slightly exceeding length of body, narrow, thin, translucent, so that nerve loop is visible.

Body wall tanslucent, marked by eight narrow longitudinal muscular thickenings which appear light gray against the darker and much broader areas between them. There are a middorsal and midventral

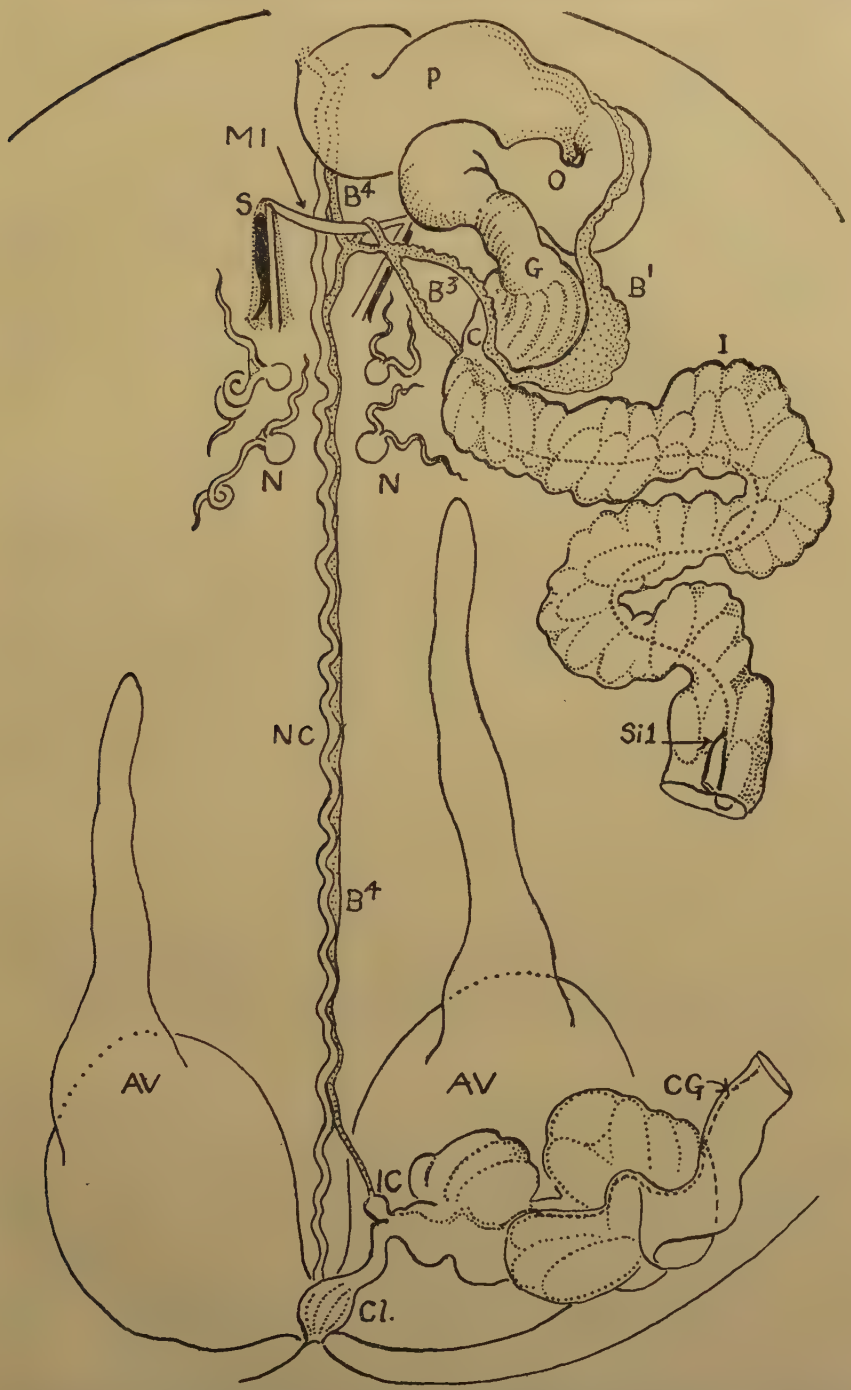

FIGURE 12.—*Listriolobus pelodes*, new species: Small specimen, × 15, showing arrangement of organs. The greater part of the intestine has been removed. In this specimen the nephridia are very small. Lettering as in figure 11.

band and three lateral, equidistantly spaced. The bands, 1.5 to 2 mm. broad, represent concentrations of longitudinal muscle fibers, which gradually thin out on the sides of the bands. The skin is beset with small, unequal, subcircular and elliptical glandular thickenings arranged in transverse close-set lines. At posterior end there is an area of greatly enlarged papillae. Coelomic surface of body wall smooth; innermost layer of slightly oblique muscle fibers very thin, uniform, not interrupted by the longitudinal thickenings of the middle layer.

Setae 2, close together, and close to the mouth. Sometimes two setae occupy one of the sheaths, with a single normal one in the other. There is an interbasal muscle uniting top of the sheaths. This passes through a loop in the dorsoventral blood vessel.

Nephridia 4, variable in size. In the type the anterior pair is smaller than the posterior, but in another specimen the anterior pair is the larger and the four are about five times the length of those of type. They have the same terminal slender portion, which can undoubtedly be expanded. Both specimens are males. The anterior pair is situated posterior to setae about the length of the latter. The ciliated funnel has long coiled lips and is attached to the outer side of the base of nephridium by a short stalk. In a third specimen the nephridia are empty and reduced to filaments slightly expanded at base. In a full-grown female (Tomales Bay) the nephridia are 20 mm. long, slender, and contain numerous eggs (June 7), 0.08 to 0.09 mm. in diameter.

Anal vesicles 2, variable in size, capable of great extension. Each is fastened to body wall about 5 mm. laterally from the anus by one or two mesenteries and ventrally by another pair close to nerve. Into these, which appear hollow, extends a short diverticulum of the vesicle. There are scattered, very tiny, ciliated funnels. The well-preserved female from Tomales Bay has vesicles that extend as far forward as the large posterior nephridia and lack the basal diverticulum found in the male.

Alimentary canal. The pharynx extends to the sharp bend shown in the illustration, followed by the esophagus. The gizzard is short and the stomach relatively long, but there is bound to be variation in different specimens owing to the accidents of preservation. The intestine proper starts just back of the ring blood vessel, at the beginning of the ciliated groove, which soon becomes differentiated into the siphon. Even in the carefully hardened specimen from Tomales Bay the intestinal wall is delicate and transparent. The length is difficult to measure on account of unequal contraction. The siphonal part is on the order of 100 mm. in length and the postsiphonal 125 mm. (length of specimen, 40 mm.). Throughout its length the intestine is stuffed with small unequal (1–2 mm.) ellipsoidal mud pel-

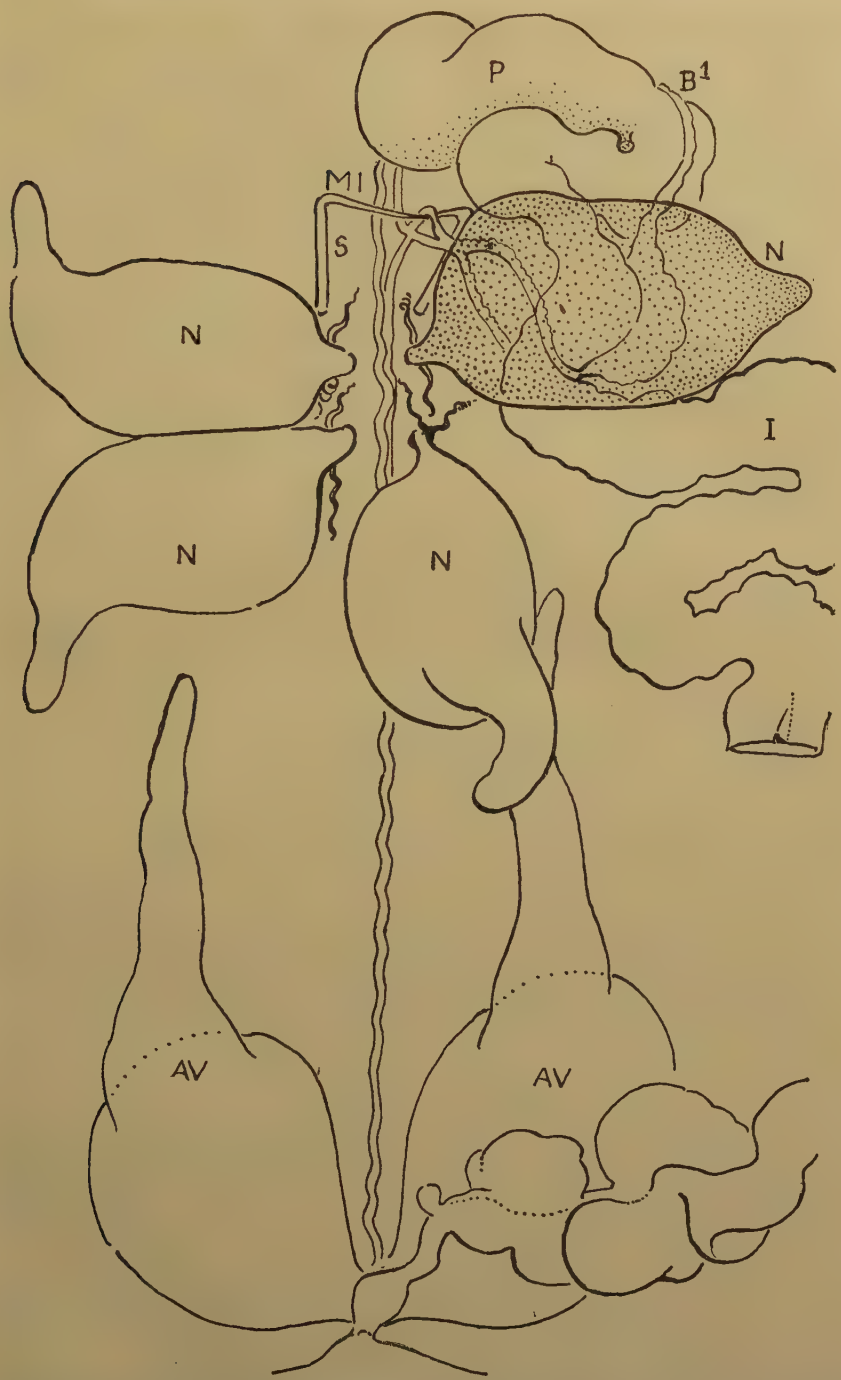

FIGURE 13.—*Listriolobus pelodes*, new species: A sexually mature but small female, showing nephridia greatly swollen by contained eggs (not indicated), × 15. Lettering as in figure 11.

lets. Just before the hind-gut passes into the small cloaca there is a spherical ventral coecum, to which extends the ventral blood vessel.

The vascular system can be readily followed on plate 22. The neurointestinal connective forms a loop around the interbasal muscle of the setae. The two flaplike expansions of this vessel, shown in the figure, are not present in the Tomales Bay specimen. The dorsal vessel varies widely in diameter being sometimes greatly inflated (Tomales Bay), the inflation extending into the neurointestinal connective.

Owing to the very thin, translucent body wall the nerves can sometimes be seen under strong illumination such as sunlight. They pass directly around the body, from the ventral nerve cord, without visible branches. The translucent proboscis affords an opportunity to trace the proboscis loop throughout its entire course (pl. 21, fig. 2). This ganglionic continuation of the ventral cord is near the margin of the proboscis, to which numerous tiny nerves pass from slight ganglionic thickenings on the outer side of the cord. No nerves, under favorable conditions, could be detected on the mesial side of the cord.

Color in life: "Proboscis yellow orange, deepest on edge; body dull grey-violet with greenish raised specks about 0.5 mm. in diameter, spaced quite regularly about 0.5 mm. apart (the papillae); 8 lighter colored muscle bands" (large specimen from Tomales Bay).

Small phase (figs. 12, 13; pl. 21, figs. 4, 4a–b). Small examples are fairly common on muddy bottom in moderate depths off southern California and in Newport Bay. These preserve badly unless special care is exercised. They are usually strongly contracted into subspherical form and vary greatly in appearance. Sometimes the body wall is rather uniformly transparent but more often the posterior portion is opaque. This region may be smooth or thrown into eight meridional swellings which occasionally extend the whole length, giving the appearance of a tiny melon. These swellings are caused by the contraction of the eight muscle bands and are found in strongly contracted specimens 7 mm. long. But specimens in which the body wall is stretched and transparent do not show indications of differentiated muscle bands until much later—at a length of about 15 to 20 mm. In the very small sizes the muscles are likely to show first posteriorly and ventrally. A specimen 20 mm. long from 55 fathoms off Santa Cruz Island has the 8 bands fully developed. Even in large specimens (40 mm.) the bands are not always equally conspicuous.

I have found a specimen 7 mm. long sexually mature. Normally these small examples are transparent in the midregion so that the nerve cord, intestinal pellets, and egg-laden nephridia can be plainly seen as yellowish bodies in life. The intestine is characteristically thin-walled, transparent, and highly convoluted and taxes the capacity of the body cavity. Its walls are greatly distended with mud pellets

about 1 mm. long. A specimen from Los Frailes, Baja California, has the intestine distended with sand not in pellets.

The specimen shown in plate 21, figure 4, was 12 mm. long and 9 mm. thick when alive, contracting to about 10 by 10 mm. when killed. The transparent areas of body wall are characteristic and are dotted with grayish or whitish papillae. In life the general tone is greenish or olive, with gray papillae spots, the proboscis bordered with yellow. In the clear area the lateral nerves can be seen as they leave the ventral nerve cord and in favorable specimens the nerve loop can be traced around the entire margin of proboscis.

Dr. Olga Hartman describes small specimens from off southern California as being rich, dark, satiny green in life, while those from Newport Bay Professor MacGinitie found to be decidedly greenish.

Text figures 13 and 14 indicate how widely the nephridia vary in size. In the swollen state the wall is perfectly transparent and excessively thin and the proximal parts of the four vesicles adhere to each other, the distal part lying at random, crowded amid the close coils of the mud-filled intestine. The eggs are suspended in a thin gel, spaced 1 or 2 diameters apart. They vary from 0.09 to 0.1 mm. in diameter and are grayish in color, surrounded by a clear zone (about 0.009 mm. thick). The clearly visible nucleus is 0.045 mm. in diameter.

In text figures 12 and 13 the vascular system is shown in a contracted state. It does not differ in essentials from that of the fully adult (pl. 22).

Type.—U.S.N.M. No. 20608.

Type locality.—Monterey Bay, Calif., moderate depth, fine sand; from stomach of flounders.

Specimens examined.—As follows:

Monterey Bay, 10 large and 4 small specimens.
Tomales Bay, Marin County, Calif., low tide, soft black sandy mud, about 6 inches below surface, 1 large female, June 7, 1941 (University of California).
Newport Bay, Calif., 7 to 20 fathoms, numerous specimens, 4 to 15 mm.; collected by Prof G. E. MacGinitie.

The Allan Hancock Foundation tendered for examination an important collection from Baja California and off southern California, comprising the small phase and some of intermediate size (20 to 40 mm.):

Baja California

Los Frailes, 5–15 fathoms, sand and algae, 1 specimen.
Upper end of Gulf of California, 21 fathoms, brown mud, 6 specimens.

California

Off Newport Beach, 50 fathoms, mud, 7 specimens.
Off Laguna Beach, 25–57 fathoms, sandy mud, 25 specimens.

Off Bluff Cove (8 lots) 25–100 fathoms, mud, fine sand, 32 specimens.
Off Redondo Beach (15 lots), 10–120 fathoms, mud, fine sand, coarse sand and mud, 44 specimens.
Off Point Vicente Lighthouse, 17–40 fathoms, coarse sand and mud, 4 specimens.
Off Portuguese Point, 16–20 fathoms, gray sand and seaweed, 2 specimens.
Cortes Bank, 60 fathoms, sand, broken shell, 3 specimens.
Off Point Mugu, 26–30 fathoms, mud, 2 specimens.
Santa Catalina Island, 50–51 fathoms, mud, 3 specimens.
Santa Cruz Island (5 lots), 31–138 fathoms, mud, sand, 15 specimens.
Santa Rosa Island, 28–45 fathoms, 5 specimens.
San Miguel Island, 35 fathoms, mud, 20 specimens.

Remarks.—The type and largest specimens were recovered from the stomach of flounders from moderate depths of Monterey Bay. In nearly all the examples the intestine is disintegrated and the body cavity filled with pellets of fine sand. This is true also of specimens from southern California, which were dredged and placed almost at once into alcohol.

After the drawings and description were completed I received from Prof. S. F. Light a carefully hardened specimen from Tomales Bay, collected at low tide, in mud frequented by the clams *Schizothaerus nuttalli* and *Macoma secta*. This specimen (June 7) was apparently laying eggs as the nephridia are partly emptied. It is especially valuable as it gives the characters of the adult female, is much better preserved than the Monterey specimens, and affords opportunity for recording the life colors of a large example.

In the type specimen, near the anterior left nephridium is a light-colored lobed mass (pl. 22, *x*) adherent to body wall. It is possibly a parasite.

Genus OCHETOSTOMA Leuckart and Rüppell

Ochetostoma Leuckart and Rüppell, 1828, pp. 7–8 (type, *O. erythrogrammon* Leuckart and Rüppell).—Spengel, 1912c, p 316.

Diagnosis.—Greater part of the thickness of the longitudinal muscle layer segregated into separate longitudinal bands. The intervals between these bands is crossed by very numerous separate small muscle bundles of the inner oblique layer, which remains for the most part continuous and unbroken over the surface of the longitudinal bands. Anterior nephridia, 1 to 4 pairs, the coelomic aperture having spirally coiled lips; with or without coecum at end of intestine; interbasal muscle of setae present or absent; two ventral anterior hooked setae; no anal setae.

Remarks.—The list of species that follows is mostly derived from literature and is in nowise intended to be a revision, for which specimens and new dissections will be absolutely essential. Most of the species were described as *Thalassema*. *Th. exilii* (Fritz Müller) Lampert, which has 8 to 10 muscle bands and two pairs of nephridia,

with nephrostome lips merely folded and crinkled, but not elongated, is possibly a *Lissomyema*.

a^1. Five pairs of nephridia, 3 rather poorly developed, in front of setae; 19 muscle bands ---------- **O. hornelli** (Prashad)
Five or four pairs of nephridia, 2 in front of setae; 10 or 11 muscle bands. **O. bombayensis** (Prashad and Awati)

a^2. Four pairs of nephridia, posterior to setae.
10 muscle bands ---------- **O. decameron** Lanchester
20 muscle bands ---------- **O. kempi** (Prashad)

a^3. Three pairs of nephridia, the first pair opening in front of the ventral setae the second and third pairs posterior to setae.
14 muscle bands ---------- **O. erythrogrammon** Leuckart and Rüppell[9]
15 or 16 muscle bands ---------- **O. stuhlmanni** (Fischer)[9]
15 to 17 muscle bands ---------- **O. leptodermon** (Fischer)[9]
16 to 18 muscle bands ---------- **O. caudex** (Lampert)[9]
17 or 18 muscle bands ---------- **O. kokotoniense** (Fischer)[9]
17 or 18 muscle bands ---------- **O. griffini** Wharton

a^4. Two pairs of nephridia.
7 or 8 muscle bands; papillae white, scattered uniformly all over body; color white in alcohol; proboscis one-third to one-half length of body; anal vesicles broad and saclike. ---- **O. formolosum** (Lampert)
8 muscle bands.
With incipient gills on edge of proboscis at base; broad smooth zone around anus ---------- **arkati** (Prashad)
No branchial fringe to proboscis; no smooth zone at posterior end of body; color in life greenish, in alcohol grayish flesh color; proboscis one-third to length of body. **octomyotum**, new species
10 or 11 muscle bands ---------- **O. hupferi** (Fischer)
13 muscle bands; proboscis longer than body; anal trees one-fourth length of body ---------- **O. pellucidum** (Fischer)
14 muscle bands; anal trees more than one-half body length. **O. manjuyodense** Ikeda
17 to 19 muscle bands; proboscis shorter than body; color dark green with violet longitudinal stripes and with white papillae scattered all over the body; anal vesicles long, brown, pointed anteriorly, bearing short branched outgrowths ---------- **O. baronii** (Greef)
16 or 17 muscle bands; proboscis deciduous, can equal length of body; setae with interbasal muscle; anal vesicles without branched outgrowths ---------- **O. edax**, new species

OCHETOSTOMA OCTOMYOTUM, new species

PLATE 21, FIGURE 3; PLATES 23, 24

Diagnosis.—Skin translucent, with eight more opaque longitudinal stripes marking the muscle bands, and closely stippled everywhere with very small, unequal, often elliptical glands which increase in size very markedly over the posterior region (where the muscle bands fuse into a continuous sheet); proboscis thick and fleshy in preserved

[9] Sato, 1939, p. 357 considers these five, along with *Thalassema palense* Ikeda, 1924, to be all one species, for which *erythrogrammon* is the oldest name.

specimens, varying from less than one-third to the full length of body. Four nephridia, the nephrostome with very long coiled lips. Siphon begins a short distance behind the ring blood vessel (marking the boundary between foregut and intestine); anal vesicles long, with pointed apex and with tiny ciliated funnels scattered over surface; setae without interbasal muscle. Length of full-grown specimen 110 mm.; proboscis 30 mm.; diameter 20 mm. A specimen collected at Cabrillo Beach, San Pedro, Calif., is 95 mm. long; proboscis 93 mm.

Description.—Longitudinal muscle bands 8, well developed, broader than the intervals between, rather iridescent and situated as a mid-dorsal, midventral, and (twice) three laterals. These fuse into a continuous sheath on the posterior part of body, equal to about one-third body length of expanded specimens and less of contracted ones. Anteriorly they remain separated to the base of proboscis. The innermost or oblique muscles are well developed, and between the longitudinal muscle bands they form a consecutive series of oblique partitions alternating with narrow compartments. At the bottom of these compartments is a thin layer of the longitudinal middle sheet. In the posterior region the oblique fascicles become less and less distinct as the anal area is approached. In reality the uninterrupted layer of longitudinal muscles is covered by a continuous inner layer of oblique muscles differentiated into thicker and thinner portions. Thus, forward from the anus the gradual differentiation of the separate oblique strands can be easily seen. In severely contracted specimens this posterior region does not show to advantage.

Anterior nephridia, 2 pairs, the ducts piercing the midventral muscle about midway between its outer margin and the nerve cord. The anterior pair is situated a short distance behind the setae (rather less than length of seta). The interval between first and second is a little more than twice the distance. They open internally by ciliated funnels having very long, coiled, extensible lips.

Anal vesicles 2, unbranched, capable of great distension. They open on the ventral surface of cloaca. Tiny scattered ciliated funnels may be seen on the surface.

Alimentary canal. There are three general regions: (1) An anterior division or foregut, in which the longitudinal musculature lies outside the circular musculature; (2) an intestine proper, in which this order is reversed, characterized by the presence of the ciliated groove and along a part of its course by the collateral intestine or siphon; and (3) a short rectum, or cloaca, posterior to the coecum.

The foregut consists of the pharynx, esophagus, gizzard, and stomach, and the junction with intestine coincides with the position of the ring blood vessel. The pharynx has a tough wall, rather iridescent with wavy longitudinal lines; the esophagus is thin-walled and convoluted, while the gizzard and stomach, both brief, can be differen-

tiated by texture. The gizzard is marked by circular lines, the stomach by longitudinal representing the longitudinal folds of the lining. Complicated dorsal and ventral mesenteries attach the pharynx and esophagus to body wall.

The intestine is, as usual, highly convoluted but when partly unraveled is seen to have a principal posterior loop, and then an anterior. The siphon, or collateral intestine, begins a short distance behind the ring blood vessel, its course being shown in plate 23, figure 1, where the dotted line indicates the ciliated groove, which terminates at the coecum. The walls of the cloaca have thick longitudinal folds. The anal vesicles empty into it by very small pores.

Blood-vascular system. The dorsal vessel, intestinal ring vessel, dorsoventral connectives, and ventral vessel are shown in plate 24. The ventral vessel, which anteriorly follows a part of the free edge of the ventral mesentery, terminates posteriorly on the wall of the coecum.

Color in life, greenish; in alcohol grayish flesh color with eight dark grayish stripes.

Type.—U.S.N.M. No. 20607.

Type locality.—Newport Bay, Orange County, Calif., January–February 1930, G. E. MacGinitie, 11 specimens.

Other material examined.—Cabrillo Beach (San Pedro), Calif., 1 specimen, W. R. Lloyd, Cabrillo Beach Marine Museum.

Remarks.—Newport Bay, where Professor MacGinitie collected the type series, is a rather small tidal inlet south of Long Beach. The worms were taken from a sandy bar, exposed at low tide, where they inhabited U-shaped burrows, the mouths of which were 12 to 14 inches apart and the bottom 10 to 12 inches below the surface. A mutilated specimen was dredged in 25 fathoms.

This sand bar was later removed in order to deepen the harbor, and the species was apparently wiped out at that locality as it has not since been taken in spite of much collecting.

The food consists of very fine detritus, which in the intestine is formed into ellipsoidal pellets 2 to 2.5 mm. long by 0.75 mm. thick.

The only species with which *O. octomyotum* might be confused is *O. formolosum* (Lampert) from the Philippines and Shanghai. This is a small form averaging 30 mm. in length, proboscis 8 mm., and diameter 10 mm. The color is white in alcoholic specimens, the skin very thin, with white papillae scattered uniformly all over the body. The anal vesicles are described as broad saclike organs. The species has seven or eight muscle bundles, two pairs of nephridia with spirally coiled openings, and a spherical diverticulum on the rectum—characteristics of *octomyotum*, except the number of muscles which is constantly eight in the California species.

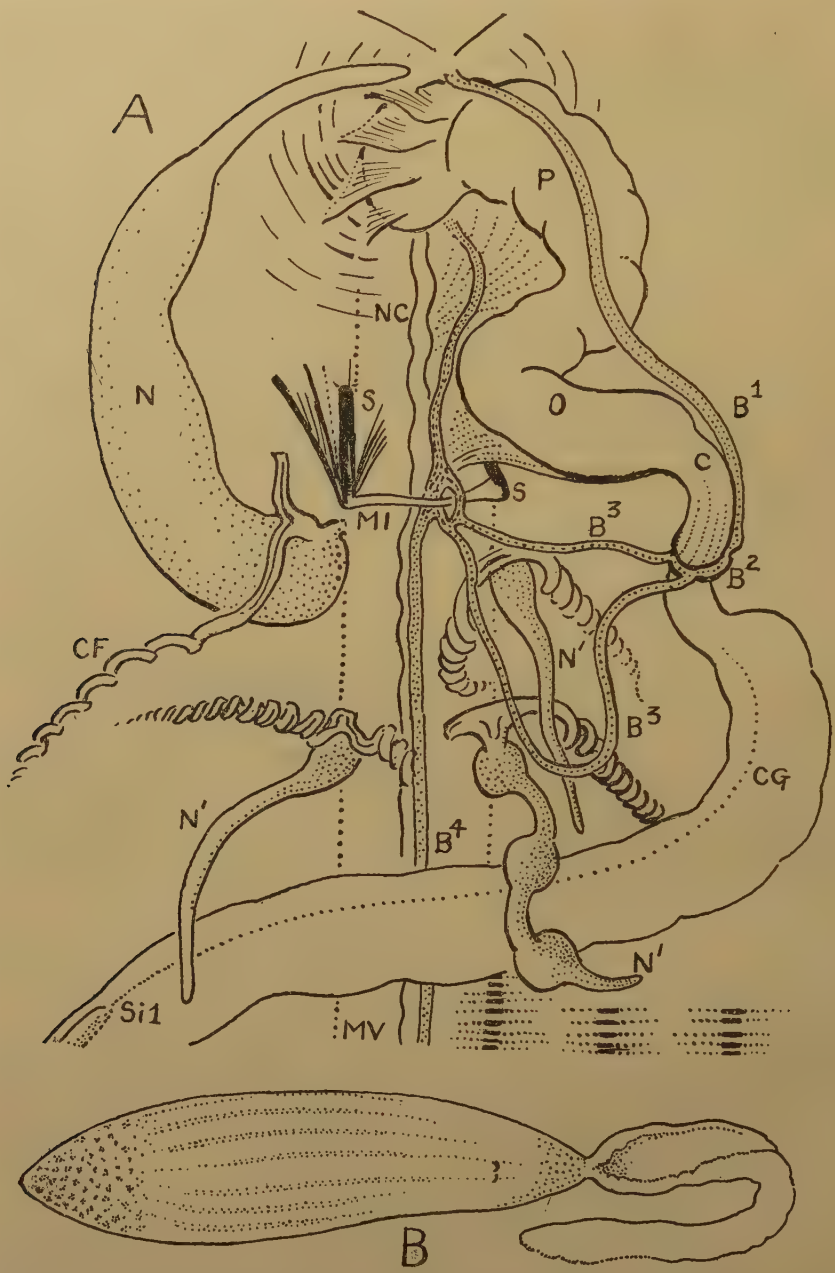

FIGURE 14.—*Ochetostoma edax*, new species: A, Dissection of anterior portion of body to show relations of nephridia, setae, vascular system, and anterior part of alimentary canal, × 6. B, Ventral view of specimen from Puerto Refugio, × 2. (*N*, nephridium similar to the four of type, a male; N^1, female nephridia from a smaller, Puerto Refugio, specimen. Other lettering as on plate 24.)

The specimen from the Cabrillo Marine Museum was taken in sand and is notable for the 93-mm. proboscis, which is 16 mm. broad near the base. The nerve loop, following the margin, is plainly visible.

OCHETOSTOMA EDAX, new species

FIGURE 14

Diagnosis.—Two pairs of nephridia situated posterior to setae, the nephrostome with spiral lips; setae with interbasal muscle passing through a small loop of the neurointestinal blood vessel; longitudinal muscle bands 16 or 17, with very narrow interspaces; rather long presiphonal intestine; precloacal coecum; two unbranched anal vesicles capable of great distension. Body wall translucent in middle region, striped with narrow dark zones; skin papillae numerous, sometimes whitish, in not well-defined transverse lines, and usually larger on posterior third or fourth of body, but not hard to the touch; proboscis deciduous, fleshy, from one-fourth to body length. Length of body 25 to 50 mm.

Description.—The 16 or 17 muscle bands merge into a continuous sheet in the posterior fourth of body. The intervals between the bands are narrower than in *octomyotum* and transverse oblique fascicles of the inner layer are decidedly weaker. The ventral muscle band under the nerve cord is broader than the others. Sixteen is probably the normal number of bundles, the extra band arising from the incomplete splitting of one of the lateral or dorsal bundles.

Nephridia 2 pairs, opening at outer margin of midventral muscle and varying greatly in size. In a male the nephridia are very large, the posterior reaching to posterior end of (contracted) specimen, while in a smaller female they have the relative size of the three smaller nephridia of figure 14. The ciliated funnel on the anterior face of nephridium has long coiled lips. The two anal vesicles, without branches, are covered with ciliated funnels and are capable of being distended to a large size. They are as long as the body in the largest specimen, which is, however, strongly contracted.

ALIMENTARY CANAL. Foregut relatively short, ending with the ring blood vessel (B^2). Only two parts are clearly differentiated, the pharynx-esophagus and stomach, with longitudinal folds. The gizzard of *O. octomyotum* appears to be lacking. The intestine is long, highly convoluted, with a very much longer presiphonal segment than in *octomyotum*, being longer than the foregut. The wall is thin and in the type is greatly distended with coarse sand; in another specimen, with sizable fragments of shells and miscellaneous hard debris. In the type the presiphonal intestine measures roughly 30 mm., the siphonal part 120 mm. and postsiphonal 90 mm. The

latter has a ciliated groove terminating at the coecum just in front of the cloaca. The walls of the coecum are much thinner than in *octomyotum* and lack heavy longitudinal folds.

Blood-vascular system (fig. 14, B^1–B^4). This is on the same plan as in *octomyotum*, but in two specimens the left dorsoventral connective from the ring vessel was much longer than the right. Passing through the small loop where these connectives join the ventral vessel is an interbasal muscle of the setae, not present in *octomyotum*. The ventral vessel ends posteriorly in the coecum without branching.

Color. "Specimens were elongate to grape-shaped, smooth and thin-skinned, greenish, with obvious and comparatively large spoon-shaped proboscis" (Steinbeck and Ricketts).

Type.—U.S.N.M. No. 20606.

Type locality.—Gulf of California: Pichalingue Bay, near La Paz, Baja California, February 1920, Luis G. Rubio.

Specimens examined. As follows:

Coronado Island, Gulf of California, March 27, 1940, Steinbeck and Ricketts, 3 specimens, under and among slightly subtidal rocks on white sand.

Point Lobos, Espíritu Santo Island, Baja California, March 3, 1940, Steinbeck and Ricketts, 1 specimen, under boulders of tide flats.

Puerto Refugio, Ángel de la Guarda Island, April 2, 1940, Steinbeck and Ricketts, 10 specimens; under boulders on beach. All these are smaller than the type.

Same locality, Allan Hancock Foundation, 1 specimen.

Remarks.—The type is without proboscis. The sketch of the entire animal is from an example taken at Puerto Refugio. As some of the specimens lack a proboscis and others have only a small one it is probable that the organ is soon regenerated. The wide difference in size seems hardly to be due to accidents of fixation.

The great disparity in size of the nephridia in the two specimens dissected shows that size is of no particular value as a character, depending as it does on the amount of contained material. There is a wide difference also in the size of the anal vesicles in the two specimens.

O. edax feeds upon the sand or coarser material in which it lives. This is not molded into definite fecal pellets. The specimen from Puerto Refugio had eaten very coarse material, which formed irregular masses in the intestine. Among the miscellaneous material could be recognized fragments of pelecypod and gastropod shells and small whole gastropod shells; serpulid tubes, calcareous bryozoans, barnacle shells; chelae of small crab; fragments of crab carapace, sea-urchin spines, and brown algae; many straight siliceous sponge spicules and fragments of volcanic rock. Some of the sponge spicules were in bundles. Others had perforated the intestinal wall and were lying in the coelomic cavity. A few were in the anal vesicles.

In the list of species, *edax* is next to *baronii*, which has 17 to 19 muscle bands and anal glands which are described as having short branching outgrowths.

In July 1918 I collected at English Harbor, Antigua, B. W. I., a small *Ochetostoma* that has 19 muscle bands, 2 pairs of nephridia, a strong interbasal muscle passing through a loop of the dorsoventral blood vessel. The anal vesicles are long, reaching to the anterior end of the contracted specimen and are covered with ciliated cups, but there is nothing that can be interpreted as branched outgrowths. The proboscis is much contracted, fleshy, and very adherent. The posterior papillae are white, conspicuous, crowded, so that they are in contact, and are hard to the touch. In a section of the body wall they resemble calcareous nodules. This posterior part of the body is perfectly opaque while the rest is slightly translucent. This species is perfectly distinct from *edax*, and it is noted here because outwardly it would pass for *O. baronii*. The specimen is a mature female with the four nephridia enlarged and full of eggs. Length of body, much contracted, 20 mm.; thickness, 9 mm.; proboscis, 8 mm.

Genus ARHYNCHITE Sato

Arhynchite Sato, 1937, p. 142. (Type, *Thalassema arhynchite* Ikeda.)

Diagnosis.—Differing from *Thalassema* in absence of a proboscis; nephridia 2, with spiral lobes to nephrostome; no intestinal coecum; no ring vessel around foregut at end of dorsal vessel, the connection between dorsal vessel and neurointestinal connective being indirect as in *Bonellia*; muscles of body wall smooth with no concentration of fibers in either the middle, longitudinal layer or in the inner, oblique layer.

ARHYNCHITE INAMOENUS, new species

Plate 25

Diagnosis.—Differing from *A. arhynchite* (Ikeda) in having a relatively longer neurointestinal blood vessel, which does not embrace the interbasal muscle. Intestine very long, especially presiphonal segment; dorsal blood vessel slender, not connecting directly with neurointestinal vessel, which is relatively long and divided into two before joining ventral vessel; size medium; skin with low papillae.

Description.—Length of type, much contracted, 70 mm.; diameter 25 mm. Skin roughened by low, close-set, pustulate verrucae largest and most irregular at ends of body. Setae 2, close to the much contracted anterior end; 11 mm. long, the inner ends united by an interbasal muscle which does not pass through loop of neurointestinal vessel.

Coelomic surface of body wall perfectly smooth and with satiny sheen, the muscles continuous, without trace of differentiation into

longitudinal or oblique bands. Where the seta muscles join body wall there are a few transverse thickenings of inner layer.

Nephridia 2, inserted close to nerve and posterior to seta about the length of latter. In the only female dissected these nephridia are four-fifths length of body and contain numerous eggs. In the male they are about one-fifth length of body and contain sperm. The internal opening (nephrostome) is on a short peduncle near base, with an irregular small lip lacking any trace of spiral structure.

Anal vesicles 2, simple, thin-walled, opening into small cloaca having longitudinally plicate walls. Minute ciliated funnels are scattered over the surface.

Alimentary canal excessively long (600 mm.) with very numerous coils attached to body wall by a multitude of very delicate frenula in which is entangled coagulum containing numerous eggs and brown bodies of unknown nature. The pharynx-esophagus is thin-walled. Plate 25, figure 3, shows the anterior complex more or less in situ and figure 4 with the interbasal setae muscle cut and the pharynx-esophagus pulled to right. The gizzard is about 6 mm. long, but the length of the stomach cannot be determined on account of condition of material. The interval between gizzard and beginning of siphon is the astonishing distance of 170 mm. The siphon accompanies the following 240 mm. of intestine, while the terminal, postsiphonal portion is 190 mm. There is no intestinal coecum in front of the cloaca.

Vascular system. The dorsal vessel can be traced posteriorly nearly to the point where the long neurointestinal connective (B^3) is attached to the lower side of the alimentary canal. The relation is similar to that of *Bonellia*. Anteriorly the neurointestinal connection divides into two branches before joining the ventral vessel. There is therefore no enlarged "heart" at the posterior end of dorsal vessel, nor a ring vessel embracing the gut at that point.

Type.—U.S.N.M. No. 20615.

Type locality.—Monterey Bay, Calif., 35–40 fathoms, mud, December 3, 1931, 3 specimens.

Other material examined.—Off southern California (13½ miles south of Seal Beach), 215–225 fathoms, green mud, Allan Hancock Foundation, 1 specimen.

Remarks.—The specimens are in a poor state of preservation, the alimentary canal being soft.

The outstanding features of *inamoenus* are the two nephridia, the internal aperture of which does not have spirally twisted lips; the extraordinarily long presiphonal gut, and the very long neurointestinal connective not embracing the interbasal muscle of setae. The vascular system lacks a definite intestinal ring vessel—probably a generic feature. *A. inamoenus* differs from the only other recognized species, *arhynchite* of northern Japan, in respect to the neurointestinal vessel

already mentioned, and in the probably much longer presiphonal gut. Details of the gut are lacking in Sato's figure and description.

Family BONELLIIDAE Baird

Bonellidae Baird (name only), 1868, p. 111. (Includes *Thalassema* and *Bonellia*.)

Diagnosis.—Dimorphic echiuroids. The male is degenerate, planarianlike, with ciliated ectoderm, generally one, exceptionally two, nephridia [10] serving as sperm receptacles, and a vestigial alimentary canal; it lives semiparasitically or parasitically on or in the female,[11] and is sometimes absent from female; females resembling *Thalassema* but with bifid proboscis in some genera; two, four, or exceptionally many anterior ventral setae are sometimes present; no anal setae; anal vesicles with many branches ending in ciliated cups; one to three nephridia.

KEY TO GENERA OF BONELLIIDAE

a[1]. With an elongate proboscis bifid at the end.
  b[1]. With ventral setae [12] or hooks a short distance behind mouth.
    c[1]. Regularly one nephridium or egg receptacle (either right or left).
      d[1]. Coelomic aperture of nephridium (i. e., the nephrostome) situated near base of the organ, usually at end of a short lateral tube. **Bonellia** Rolando
      d[2]. Large nephrostome at extreme distal end of nephridium and not facing laterally ..... **Bonelliopsis**, new genus (p. 252)
    c[2]. Regularly 2 nephridia, having the small nephrostome laterally near distal end; a small blind tube opening between nephridiopores serving as a permanent androecium for completely parasitic male; gonad of female situated on frenula radiating from cloaca; anal vesicles in form of tubules opening independently into cloaca (see also *Acanthohamingia*) ..... **Pseudobonellia** Johnston and Tiegs [13]

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[10] Males of *Pseudobonellia* have two nephridia; other genera one only.

[11] The male lives in the foregut, in nephridium, on proximal portion of proboscis, in genital groove (*Acanthohamingia*), and in a specialized blind tube or androecium opening between the two nephridiopores (*Pseudobonellia*).

[12] In *Bonellia miyajimai* Ikeda (1904, p. 73; 1907, p. 2, pl. 1, figs. 1, 2; pl. 2, figs. 5–17) there are numerous (29) very small setae. *Pseudobonellia* has two to four setae; *Archibonellia* has four and other genera have two setae, but sometimes a complemental smaller seta is in process of growth and later replaces the functional one.

[13] Johnston and Tiegs, 1919, pp. 213–229, pls. 9–11. This is a very remarkable genus set apart from all other bonelliids in having a small blind tube, projecting into coelom and opening on the ventral body wall between the two nephridiopores by a narrow canal whose walls contain strong sphincter fibers. In this lives permanently one very degenerate male, its posterior end grown fast by enlarged ectodermal cells to the much smaller epithelial cells of the tubule. The male lacks setae and has two sperm receptacles, differing from all other known males (which have only one). The ovary is entirely different from that of other genera. "The mesenteric strands of muscular tissue which maintain the posterior portion of the rectum in position are very well developed and form the basis of the ovary whilst from the peritoneum lining them the ova are developed" (p. 221). "The anal glands or posterior nephridia are represented by two small, tuft-like masses situated one on each side of the posterior end of intestine. Each consists of a mass of very delicate, simple, cylindrical tubes opening separately into the rectum, whose walls in this region are thickened. The tubules are approximately circular in section with an irregular lumen. They consist of a single layer of epithelial cells. Near its free end each tubule becomes narrowed before opening into the coelom by a slightly dilated funnel fringed with long cilia" (p. 220).

This species was collected in the Capricorn Group, Great Barrier Reef, due east from Keppel Bay, Queensland. Subsequently Monro (1931, p. 33) reported the species from Low Isles.

c^3. Three nephridia, an unpaired between a pair; ovary along nerve cord; anal vesicles: a fascicle of tubules at end of a collecting tube.
Archibonellia Fischer [14]

b^2. No setae present.

c^1. Nephrostome situated at end of a short lateral tube near blind distal end of nephridium ..... **Parabonellia** Onoda

c^2. Distal end of nephridium expanded into plicated rim of large nephrostome ..... **Eubonellia**, new genus (p. 255)

a^2. Proboscis when present similar to that of *Thalassema* and not bifid at extremity.

b^1. No sharply marked groove between nephridiopore and mouth.

c^1. Female with 2 well-developed ventral setae; anal vesicles 2, elongate, dendritic; nephrostome near base of the single nephridium; male unknown ..... **Protobonellia** Ikeda

c^2. Female with 2 ventral setae; nephridia 2, large, with basal 2-lipped nephrostome; anal glands wide sacs provided with a very large number of slender excretory tubules with apical funnel; male unknown.
Maxmülleria Bock

c^3. No ventral setae in female.

d^1. Proboscis deciduous, *Thalassema*-like; 2 external papillae marking nephridiopores; nephridia 2 or 1 with basal nephrostome; anal vesicles in 2 thick clusters of tubules opening into a common duct; male with ventral hooks ..... **Hamingia** Danielssen and Koren

c^4. In place of proboscis a short truncate snout; a proboscis possibly normally present; 1 nephridium with basal nephrostome; duct of nephridium passing under nerve cord and opening in median line into a funnel-shaped depression of skin; anal vesicles; numerous dendritic masses arising from a basal bladder on each side of large muscular cloaca; terminal portion of hind-gut, in front of cloaca, greatly enlarged; male unknown ..... **Nellobia**, new genus (p. 257)

b^2. A narrow, or expanded, slit extending forward from nephridiopore, in 2 species containing 8–10 tiny, integumentary spines; anal vesicles not in form of 2 dendritic structures or 2 clusters of tubules, but in form of independent branched tubes or an asymmetrical cluster; 1 or 2 nephridia with nephrostome near base; males with or without hooks.
Acanthohamingia Ikeda (p. 260)

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[14] Wilhelm Fischer, 1919, p. 283, figs. 5, 6; 1926b, p. 207, pl. 2, figs. 1–7, text figs. 1, 2. *Archibonellia michaelsoni*, the type, from a coral reef, Rottnest Island, Fremantle, Australia, is only 12 mm. long; it has a large median between and above two small nephridia (no nephrostomes were found). The proboscis has two terminal lappets instead of divisions, and the alimentary canal is short, scarcely over twice length of body. *A. mjöbergi* (1926b, p. 208, fig. 1. northwest coast of Australia), however, has a very small unpaired nephridium (with basal nephrostome) between a pair of very large "uteri" filled with eggs and with terminal nephrostome. The alimentary canal is of normal length for a bonelliid, and the proboscis is normally cleft at the tip. Fischer, in a quandry what to do with this species, places it in *Pseudobonellia* on the basis of the large paired nephridia, with terminal nephrostomes, and the normal alimentary canal and proboscis. Even though the androecium of *Pseudobonellia* may well have originated in an unpaired nephridium, the fact remains that in *Pseudobonellia* the androecium is highly specialized and is no longer a nephridium, while the ovary is not found along the nerve cord, as in *Archibonellia*, and the tubes of the anal vesicles open separately into the cloaca, not into a common duct. The two species of *Archibonellia* may not be congeneric, but the aberrant species is certainly widely different from *Pseudobonellia*.

FIGURE 15.—*Bonellia viridis:* Dissection (× 5) of anterior part of specimen from Naples to show particularly the position of nephrostome, *CF*, at base of nephridium, *N*, which was 55 mm. long while the animal was only 45 mm. Note the long segment of gut between gizzard, *G*, and beginning of siphon, *Si1*. The anterior end of gonad, *Go*, is shown. (B^1, B^3, B^4, dorsal, neurointestinal, and ventral blood vessels; *C*, stomach; *G*, gizzard; *NC*, nerve cord; *O*, esophagus; *P*, pharynx.)

FIGURE 15.—(See opposite page for legend).

BONELLIOPSIS, new genus

Diagnosis.—Differing from *Bonellia* in having the nephrostome at the distal end of the nephridium instead of near the base, and in the possession of a much shorter presiphonal foregut; either left or right nephridium developed; females with two ventral setae; males without setae.

Type, *Bonelliopsis alaskana*, new species.

BONELLIOPSIS ALASKANA, new species

FIGURE 16; PLATES 26, 27

Description.—Body elongate, subcylindrical, blunt at both ends, 20 to 65 mm. long, and commonly four or five times as long as thick; proboscis of usual *Bonellia* form seldom exceeding body length and usually considerably shorter. Contracted skin verrucose, the verrucae squarish, not obviously larger in any particular region; when skin is stretched the verrucae flatten out into squarish glandular thickenings arranged in irregular longiseries.

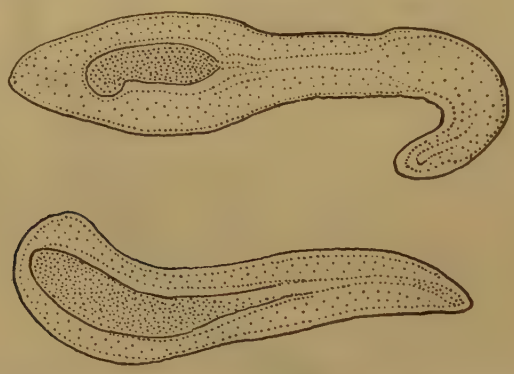

FIGURE 16.—*Bonelliopsis alaskana*, new species: Two males, the upper 1.27 mm., the lower 1.9 mm. long, × 50. The spermatheca is most heavily shaded; the lightly stippled is parenchymatous and muscle tissue; sperm duct opens at anterior (right) end.

Body wall thin, translucent. Inner, circular layer of muscles smooth, but in the region of foregut where the layer is thickest there is a division into slender fascicles.

Setae 2, small, nearly straight, situated close together a short distance behind mouth (4 mm. in specimen 44 mm. long). There is a short but broad interbasal muscle which usually presses upon the nerve cord and ventral blood vessel.

Nephridium 1; of six specimens dissected four had the left nephridium developed and two had the right. It is situated close to the nerve cord directly behind the setae. In some specimens the nephridiopore is conspicuous externally. The nephrostome is conspicuous, terminal, with amply folded lips. When the nephridium is filled

with eggs its distal end is usually invaginated, concealing the nephrostome (pl. 27, fig. 1). The mucosa is thrown into shallow longitudinal folds, most pronounced at proximal end.

The two anal vesicles have the relative size and general form indicated in plate 26, figure 1, where only one is shown. Each opens by a small pore into the cloaca. The primary branches of the vesicle vary in number. In plate 26, figure 2, is shown the tip of one of the major subdivisions including two of the smaller secondary branches, each of which bears several funnels.

Alimentary canal. As contrasted with *Bonellia viridis* the alimentary canal differs in having a much shorter foregut, especially the portion between the gizzard and the intestine, corresponding in general to the "stomach" of *Thalassema* and allies. The abruptly enlarged intestine is produced forward into a coecum where the dorsal blood vessel envelops the intestinal wall. In the specimen of *B. viridis* that I dissected this was not differentiated (fig. 15).

The pharynx is connected with the body wall by numerous radiating muscular frenula of which only a few are indicated in the figures. The mucosa is thick, verrucose, and not very different from that of the esophagus. The gizzard has stronger ring muscles than the esophagus (which shows a ringed structure), and the mucosa is thrown into consecutive ring folds. When spread out these ring folds subdivide into eight longitudinal divisions. Behind the gizzard the mucosa becomes abruptly thinner, and between the gizzard and this elongated stomach there is a sort of pyloric constriction, with a very narrow passage. The opening, on the stomach side, is surrounded by a flange of tissue. There is no presiphonal ciliated groove, but a postsiphonal one runs along the intestine to the point where the ventral blood vessel and genital stolon join the hind-gut. The fecal pellets are slender blunt ellipsoids 2.5 mm. long. In one I found an ostracod and a small *Balanus*.

Mesenteries. The mesenteries are continuous, very thin sheets, even in the postsiphonal region of the intestine. In plate 27, figure 2, an attempt has been made to show the principal mesenteries of the foregut, which are voluminous and folded when the animal is contracted. In this semidiagrammatic drawing the left half of the animal only is shown. What is probably the ventral mesentery (*VM*) is attached to body wall over a sinuous and not so smoothly regular course as shown in figure. It is fastened to the left side of pharynx-esophagus, passing gradually to the side of the intestine opposite the siphon. The posterior part of dorsal blood vessel (B^1) is attached to, or involved in, this mesentery. The dorsal mesentery (*DM*) is attached to the body wall in a long spiral passing from right side (dot and dash line) over to left side. Posteriorly it merges with the ventral mesen-

tery on its left side, where the foregut enters the intestine. In the drawing the posterior face of dorsal mesentery is shown and only a small part of the anterior (or dorsal) side adjacent to pharynx. The attachment to the gut is along the lateral line, but behind gizzard the attachment moves over near to that of ventral mesentery. A special muscular mesentery indicated in plate 27, figure 1, but omitted from figure 2, joins the gizzard to the stomach. A special transverse dorsal muscular mesentery supports the dorsal blood vessel anteriorly. When the animal is extended the effect of these mesenteries is to form a somewhat spiral anterior cul-de-sac in which the nephridium lies and in which the eggs probably congregate. But when the nephridium is full of eggs, as in plate 27, figure 1, there may still be hundreds of eggs, seemingly mature, in various parts of the coelom.

Vascular system. The distribution of the principal trunks, shown in the figures, seems to be almost the same as in *Bonellia viridis* (fig. 15). The connection between the dorsal and ventral vessels is not direct, as in *Echiurus*, *Ochetostoma*, and *Thalassema*, but by means of lacunae in the intestinal wall, as is the case in *Arhynchite*.

The gonad lying along the top of the ventral blood vessel, in the posterior half of body, seems to be identical with that of *B. viridis*.

Male. The males are found in the foregut, from the pharynx to the gizzard, in the order of about a dozen to an individual. In one case I found two or three in the anterior part of the stomach. Dr. H. Heath, who collected the type series, examined several live specimens and found no males in the nephridium.

The males vary from elongate-slender to the shortened state shown in figure 16. When fully extended they are more than twice as long as figure and only about half as thick. The sperm receptacle is situated posterior to middle of body and the duct opens at anterior end, or very close to it. There is very little free coelom, the body being filled with parenchymatous and muscle tissue, diagrammatically indicated by the more spaced dots in figure. No setae are present.

Type.—U.S.N.M. No. 20603.

Type locality.—Dutch Harbor, Unalaska, under rocks, at low tide; Harold Heath, August 1917, 15 specimens.

Specimens examined.—In addition to the above, 25 specimens, without locality, U. S. National Museum.

Remarks.—The type series was collected by Dr. Harold Heath, who found them in the intertidal zone under flat rocks. The worms were arranged around the periphery of the stone with the proboscis extended to the margin. In life the animals are light green, the color of "green prunes," which, in the contracted state, they somewhat resemble.

EUBONELLIA, new genus

Diagnosis.—Bonelliidae with well-developed bifurcate proboscis, no setae, and a single (right) nephridium, the distal end of which is expanded into the plicated rim of the large nephrostome; anal vesicles essentially as in *Bonellia;* male with sperm receptacle reaching nearly to posterior end of body; body wall thick.

Type, *Eubonellia valida*, new species.

Remarks.—This genus differs from *Bonelliopsis*, the only other known to have a strictly terminal nephrostome, in lacking setae. Its foregut has an unusually extensive stomach or crop, between the gizzard and beginning of siphon, this segment being short in *Bonelliopsis*. The mesenteries of the intestine of *Eubonellia* are in the form of strands, not a sheet.

Parabonellia Onoda, [15] based on *Bonellia misakiensis* Ikeda,[16] also lacks setae in both male and female. The nephridium has a small pedunculate funnel situated, not at the base as in *Bonellia*, but on the side of the vesicle near the terminal blind end. Ikeda did not show this in his figure of a "dissection" of the type, but it is figured by Onoda (fig. 1) and Sato [17] (fig. 2). None of these writers has figured or described significant details of the foregut, which are of importance in classification.

The body wall of *Parabonellia* is thin while that of *Eubonellia* is very muscular, but this is a character varying with the contraction of the specimen and is scarcely of generic significance.

In *Eubonellia* the male is about half the size of the male of *Parabonellia*, which is described as nematodelike, 3.3 to 3.5 mm. long, and 0.2 to 0.3 mm. in breadth. The sperm vesicle and canal occupy the anterior fifth to third of the body. In *Eubonellia* the vesicle extends nearly to the posterior end of the body, which is depressed, planarian-like.

Protobonellia Ikeda [18] (type, *P. mitsukurii*, Sagami Bay, Japan, 300 fathoms) has very strong setae with unusually well developed muscles. The proboscis is similar to that of *Thalassema*, and the single (left) nephridium is similar to that of *Bonellia*. The nephrostome is a wide fimbriated funnel at the end of a slender tube opening into the nephridium near the base of that organ. The anal vesicles are similar to those of *Bonellia* rather than *Hamingia*, which the proboscis might lead one to expect. The vascular system seems to possess a peculiarity in a rather direct connection between the dorsal vessel and the neurointestinal connective at a point immediately anterior to the beginning of the siphon. Ikeda treats this very summarily in both

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[15] Onoda 1934, p. 418 (*Pseudobonellia*); 1935, p. 141 (*Parabonellia* for *Pseudobonellia*, preoccupied).

[16] Ikeda, 1904, p. 74, figs. 24, 103–105.

[17] Sato, 1935, p. 142, figs. 1, 2.

[18] Ikeda, 1908a, p. 259, figs. 1–4.

description and figure, apparently not realizing that it is different from the relations of the two vessels in *Bonellia*. Neither his figure nor description gives any definite details concerning the foregut beyond the fact that it is very long.

EUBONELLIA VALIDA, new species

PLATE 28

Description.—The much-contracted type is oblong-cylindrical, 55 mm. long, and about 20 mm. thick at middle. The conspicuous nephridiopore is 8 mm. behind mouth. Proboscis unusually broad and flat, terminally bifurcate, without a ventral sulcus. In its contracted state it is 30 mm. long and 7–9 mm. broad (pl. 28, fig. 3). The thick skin is thrown into annular welts, the furrows being frequently interrupted. These folds do not carry marked pustulate thickenings as in the case of *Nellobia* found at the same station. From the mouth a short narrow sulcus extends upon the constricted base of proboscis.

Body wall tough and muscular, 1.5 to 2.5 mm. thick, the middle longitudinal layer being the thickest. The inner, circular layer is smooth, but somewhat fasciculated at anterior end of body.

No setae or vestiges of seta sacs or muscles.

The single large (right) nephridium has a terminal large nephrostome with voluminous lips. At the base a simple duct leads to the exterior approximately in the median line.

The two anal vesicles are of the elongate dendritic type with a voluminous axial bladder having a few branches proximally. To the main stem and branches are attached singly or in clusters (pl. 28, fig. 2) the nephritic elements, which are characteristically very elongate, ending in pedunculate funnels. The vesicles are attached to each side of a very small cloacal bulb, the mucosa of which is thrown into longitudinal ridges.

ALIMENTARY CANAL. The anterior part of pharynx is attached to body wall by numerous frenula, but there is no peripharyngeal diaphragm such as is characteristic of *Nellobia*. There is a rather delicate mesentery at the bend of the esophagus (not shown in figure). Food pellets form in the posterior part of esophagus (O^1), as well as in the gizzard (G), and are collected in the elongate stomach. The wall of the stomach is almost transparent. Between it and the gizzard there is a powerful sphincter forming a sort of pylorus as in *Bonelliopsis*. There is a weaker sphincter between the esophagus and gizzard.

There is no presiphonal ciliated groove. Much of the intestine is missing, but enough remains to show that there is an extensive portion, traversed by the siphon, which has thicker walls so that the pellets are not visible, whereas the postsiphonal intestine (with a

ciliated groove) has very thin walls and very compact pellets (pl. 28, fig. 4). The ciliated groove ends at entrance to small cloacal bulb and a strand of tissue from the ventral blood vessel is attached at this point.

The vascular system is of the usual bonelliid type and can be followed in the figure. The ventral vessel divides into two at about the point where setae would be if present.

The gonad, in the usual bonelliid position, is confined to the median third of the body and is inactive, there being no sign of egg formation. In *Nellobia*, dredged at the same time, the gonads were active and the nephridium full of eggs.

Male (pl. 28, fig. 5). One was found in the pharynx near mouth. It is possibly not fully matured; length 1.17 mm. The dark body is the sperm vesicle, the duct opening at the anterior end as in *Bonellia viridis*. The small spot back of the gonad is probably the excretory pore. Small indistinct masses of spermatozoa can be seen in the coelom, but have not been shown in the drawing. The gonad is situated more posteriorly than in *Bonellia viridis*.

Type.—U.S.N.M. No. 20604.

Type locality.—*Albatross* station 5021, Okhotsk Sea, off east coast of Sakhalin Island, lat. 48° 32′ 30″ N., long. 145° 08′ 45″ E., 73 fathoms, green mud, sand, pebbles, bottom temperature 30.9° F.

NELLOBIA,[19] new genus

Diagnosis.—Bonelliidae without setae and possibly without proboscis; one nephridium (left), with a basal nephrostome and swollen basal region, opening in the median line but without a genital groove; two compound anal vesicles each consisting of numerous trees arising from a sessile receptacle on either side of the very large muscular cloaca; terminal portion of hind-gut greatly enlarged; body wall very thick.

Type, *Nellobia eusoma*, new species.

Remarks.—This genus differs from *Bonellia*, *Protobonellia*, *Parabonellia*, *Eubonellia*, and *Bonelliopsis* in the radically different structure of the anal vesicles and from all bonelliids in the extremely large muscular cloaca and enlarged terminal part of the hind-gut. The only group which has fundamentally similar anal vesicles is *Acanthohamingia* Ikeda [20] in which three trees arise independently on each side of the cloaca (*A. ijimai*) or more numerously as a cluster with probably some connection between the elements (*A. shiplei*). In *Hamingia arctica* Danielssen and Koren [21] there is a very short (1 mm.)

[19] Anagram of *Bonellia*.

[20] Ikeda, 1910, p. 136, pl. 10; see also 1908, p. 61, pl. 1.

[21] Danielssen and Koren, 1881, p. 20, pl. 4 and 5, figs. 1–18.

tube on each side of the cloaca to which very numerous small trees are attached at approximately the same point.

The vascular system of *Nellobia* is similar to that of *Bonellia* and allies in the relation between the dorsal blood vessel and the neuro-intestinal trunk. No direct connection exists between the two by obvious anastomosis of terminal branches such as Danielssen and Koren figure (1881, pl. 5, fig. 14).

NELLOBIA EUSOMA, new species

PLATES 29, 30

Description.—The single specimen is contracted to the maximum extent. The posterior end of the body is invaginated to form a cup-shaped depression. The intestine had been extruded, after the manner of holothurians, through a breach in the cloacal wall, and most of it is missing.

Body of *Bonellia* form without proboscis, 44 mm. long (allowing for posterior invagination), and 15–17 mm. thick at middle. Owing to contraction, the skin is thrown into irregular transverse folds with frequent pustulate thickenings, less regular in the anterior ventral region (shown in pl. 29, fig. 1) than elsewhere. If the very short truncate snout is the remains of a longer proboscis, it is nevertheless covered with normal skin. The conspicuous opening of the nephridium is close to the median line about 4 mm. behind mouth.

The body wall is very muscular and in the contracted state about 2 mm. thick. The middle longitudinal layer is the thickest, the inner circular layer the thinnest. The latter in the contracted state of the specimen shows definite fascicles of uneven width which would probably smooth out when the worm is expanded.

The single nephridium (pl. 30) is attached on the left of the nerve cord, but its duct passes under the cord to open in the median line. The nephrostome has very simple lips and passes into a bulbous and thick-walled proximal region. The distal compartment, filled with eggs, has the wall stretched to translucent thinness but its proximal constricted part has glandular walls furrowed longitudinally. There is a definite opening from the egg chamber into the proximal bulbous portion.

The anal vesicles are peculiar. Instead of having a roughly treelike form as in *Bonellia* and *Bonelliopsis*, the main vesicle is a sort of crescent-shaped pouch applied to each side of the large cloacal cavity and produced on the opposite or free border into numerous (a dozen or more) unequal dendritic subdivisions. The larger of these have a few main branches like a tree, which in turn are crowded with branchlets (pl. 29, fig. 4) carrying many of the bulbous glandular elements ending each in a ciliated funnel. Around the base of these primary

nephridia are numerous subglobular unequal yellow bodies arising from the base of the nephritic elements and from the wall of the collecting tube or branchlet. Numerous much smaller brownish-yellow papillae occur on the walls of the main stems and branches. I could not find the opening into cloaca.

ALIMENTARY CANAL. The main features of the foregut are shown on plate 30. The pharynx is attached to body wall by very numerous crowded radiating strands. This head cavity is separated from the rest of coelom by a translucent diaphragm (*D*) indicated in the drawing incompletely. Its central border encircles the gut behind the pharynx, and what may be conventionally called the esophagus (extending to *X* in drawing) has the muscular walls marked by prominent ring folds which cause the mucosa to be thrown into transverse welts. This muscle layer thins toward end of esophagus and the ring becomes narrower. The segment *X–Y* corresponds to the gizzard of *Bonelliopsis*. The annulation of muscle is closer. At *Y* the canal was broken, and it is possible that something was lost as the segment between *Y* and the beginning of siphon is very short. It corresponds to the so-called stomach of *Bonelliopsis*. A tough mesentery unites loops of the esophagus, whereas in *Bonelliopsis* the thicker mesentery joins the gizzard to stomach. The esophagus has a continuous ventral mesentery attached ventrodextrally but the other mesenteric attachments to body wall are in strands or frenula.

The cloaca is bulbous, with very numerous muscular strands uniting its rather muscular wall with body wall. The anterior of these strands pass between the branches of the anal vesicles. The very expanded hind-gut seems to be more than an accident of killing, as the condition of the mucosa indicates that the walls have not been unnaturally distended. The prominent ciliated groove continues from the narrow segment (all the rest of the intestine having been lost) to the beginning of the cloaca, where a strand from the ventral blood vessel ends. There is no intestinal coecum at this point.

The vascular system is of the *Bonellia* type. The neurointestinal connective (B^3) spreads out fanwise where it joins the ventral vessel (B^4) and its walls appear to be glandular as if a part of the gonad complex. Actual ova are found as far forward as the posterior border of this fan.

The gonad is of the *Bonellia* type but extends unusually far forward.

MALE. Unknown. The foregut was quite empty, and no males were found in the nephridiopore.

Type.—U.S.N.M. No. 20605.

Type locality.—*Albatross* station 5021, Okhotsk Sea, off east coast of Sakhalin Island, lat. 48° 32′ 30″ N., long. 145° 08′ 45″ E., 73 fathoms, green mud, sand, pebbles, bottom temperature 30.9° F.

Genus ACANTHOHAMINGIA Ikeda, emended

Acanthohamingia IKEDA, 1910, p. 136. (Type, *A. shiplei* Ikeda.)

Diagnosis.—Differing from *Hamingia* in having a well-marked genital slit extending forward toward mouth from the one or two nephridiopores, this containing, in two species, 8 or 10 very small setae imbedded in the skin; anal vesicles numerous, at least not in two symmetrical clumps which arise from a very short common duct; body wall thin; proboscis (when known) similar to that of *Thalassema;* males with or without ventral setae.

Remarks.—The new species described below has necessitated an emendation of the original diagnosis since there are no minute setae in the genital groove. This groove, which extends forward from the nephridiopore, or pores, occurs in the three known species [22] and is not present in any other genus. The general habit of the three species is much the same, as they are all of delicate build. The body wall is thin, translucent when expanded, and skin papillae are poorly developed. The anal trees exhibit differences in the three species, being most alike in *A. ijimai* and *A. paradola.* These are numerous, independent, or semi-independent branched tubules, and differ from the condition in any other genus except *Nellobia.* But in *Nellobia eusoma,* which lacks any trace of a genital groove and is one of the most heavily built of all bonelliids, the anal trees spring from a bladderlike structure applied to each side of the very muscular cloaca. The rudimentary bladder figured for *A. paradola* (left side) may well indicate the last trace of a similar structure.

In *A. shiplei* and *A. ijimai* the male is long and slender and lacks setae, whereas in *A. paradola* the male is lanceolate and planarian-like and is provided with two curved setae.

ACANTHOHAMINGIA PARADOLA, new species

PLATES 31, 32

Diagnosis.—Differing from *A. shiplei* and *A. ijimai* in the absence of minute setae from the genital groove of female and in the presence of a pair of ventral curved setae in the male; nephridia 2 instead of 1; anal trees numerous, slender, sparsely branched, arising for the most part independently from the very thin wall of the cloaca. Length of paratype 90 mm. (pl. 31, fig. 1). Color, pale flesh when seen on a white background.

Description.—The general habit is much like that of *A. ijimai* but proboscis is lacking. The body wall is very thin and translucent, this thinness being accentuated by inflation. Along the midventral line the extremely slender nerve cord can be easily seen. The skin

[22] *A. shiplei* Ikeda 1910, p. 136, pl. 10; *Hamingia ijimai* Ikeda, 1908b, p. 62, pl. 1.

is marked by flat circular spaced spots slightly less translucent than the intervals. Back of the mouth is the characteristic genital groove, which normally is probably very narrow as in the type (pl. 31, fig. 3) but in the paratype (pl. 31, figs. 2, 2*a*) is spread apart owing to stretching of body wall. In this groove are four males. In the type there is at least one. At the posterior end of groove are the openings of the nephridia: two in the type and another specimen (pl. 31, figs. 4, 4*a*); one in the paratype (pl. 31, figs. 1, 2). The hemispherical papilla shown in these figures beside the nephridiopore is an artifact. Although there is but one opening there are two large nephridia containing eggs.

As stated above, the body wall is very thin, on the order of 0.15 to 0.2 mm. thick, and a single thickness is so transparent that printing can be easily read through it. The fibers of the longitudinal and circular muscles can be seen under magnification, but there are no bundles.

All three specimens are in poor condition internally as the midgut and hind-gut are badly macerated, the contained pellets being adrift in the coelom. The more essential foregut can be made out with the associated blood vessels.

The nephridia, in good condition, number two in all three specimens. They have exceedingly thin walls, and the small nephrostome and its short stalk are situated at the base, close to the swollen ducts leading to nephridiopores. In the paratype the nephridia are about twice as large as those shown on plate 32.

The significant features of the alimentary canal can be seen on plate 32. The pharynx is much inflated (but probably unnaturally) and has very thin walls. The esophagus can be traced to O^1 where the fine longitudinal ridges of the mucosa change to equally small rings. Then follows an exceptionally long segment of the foregut in which I can find no marked division into gizzard and stomach (or "crop"). In this the contents are shaped into oblong pellets 1.5 to 2 mm. long. Extremely slender and numerous frenula connect the pharynx to body wall. The continuous ventral mesentery of foregut is delicate and transparent. The position of the coils of foregut in figure has no significance as they had mostly broken moorings. All the foregut is thin-walled.

In connection with the vascular system the very considerable length of gut between attachment of dorsal vessel (B^1) and neurointestinal connective (B^3) may be noted. The ventral expansion of B^3 is considerably farther back in another specimen. In keeping with the rest of the animal the blood vessels are delicate and the ventral trunk is very inconspicuous. There are numerous opaque nodules on the neurointestinal trunk.

The nerve cord is the slenderest I have seen in a mature echiuroid, being only 0.135 mm. in diameter.

The gonad, on the irregular margin of a mesentery dorsal to nerve cord, is invisible except under high magnification, as the cells are small and inactive. The whitish eggs in the nephridia are 0.5 to 0.6 mm. in diameter.

Anal vesicles are in the form of numerous slender tubes with spaced short lateral branches (pl. 31, fig. 6). These tubes are involved in and fastened to body wall by transparent but strong frenula. In the type nearly all the tubes of the left side spring from a small irregular common chamber closely appressed to the transparent wall of the cloaca, but on the right side no such common chamber is present. Here the vesicular tubes arise independently from the cloacal wall. It is probable that the number of tubes increases with age. The ultimate subdivisions are not well enough preserved for exact delineation but they resemble in general those of *A. ijimai*. Although the cloaca is not perfect in any of the specimens, that of the type shows a rather large subspherical chamber with transparent walls joined to the body wall by a multitude of frenula.

Male. Males occur in the genital groove as shown in plate 31, figure 2. Probably the groove is normally as in the type, which has one or two males in it. They are depressed lanceolate in form, 1.2 mm. long, and the tube of the sperm receptacle opens at the middle of the anterior end, the receptacle itself being about in the middle of body (pl. 31, fig. 5).

Type.—U.S.N.M. No. 20601.

Type locality.—*Albatross* station 4942, Kagoshima Gulf, Japan, 118 fathoms, brown mud, black specks, bottom temperature 59.8° F., 2 specimens.

Specimens examined.—The above and 1 specimen (paratype) from station 4940, same locality, 115 fathoms (pl. 31, fig. 1).

Xenopneusta, new order

No blood-vascular system, the coelomic fluid being heavily charged with large blood corpuscles containing hemoglobin or hemoglobin and hematin; intestine with terminal portion in front of cloaca enlarged, thin-walled, functioning as an organ of respiration in connection with anus and cloaca.

Family URECHIDAE Fisher and MacGinitie, 1928

Diagnosis.—Differing from other Echiuroidea in the absence of a blood-vascular system, the corpuscles (red or brown in color from hemoglobin or hemoglobin plus hematin) free in the coelomic fluid; distal portion of midgut greatly enlarged and in connection with cloaca serving as a respiratory apparatus; foregut very long,

including a long gizzard between an anterior long crop and a posterior long stomach; proboscis reduced to a scoop-shaped upper lip.

Genus URECHIS Seitz

Urechis Seitz, 1907, p. 352 (type, *Echiurus chilensis* Max Müller, 1852).—Fisher and MacGinitie, 1928a, p. 200.
Spiroctetor Skorikov, 1909, p. 77 (type, *Echiurus unicinctus* von Drasche).

Diagnosis.—Cylindrical or sausage-shaped echiuroids with characters of family. Body wall is very muscular, consisting of outer and inner circular layers and middle longitudinal layer, the latter the thickest; inner layer showing a fasciculate arrangement superficially. In the region of the posterior pair of nephridia is a zone of compound slime-net glands lodged in the verrucae of the skin. There are two or three pairs of nephridia, the basal nephrostome of which has long spirally coiled ciliated lips for collection of mature germ cells. The two anterior setae have a strong interbasal muscle; one ring of curved anal setae interrupted ventrally. Traversing the coelomic cavity in front of the anterior setae are paired dorsoventral muscles (pl. 34, fig. 2, *13*). The alimentary canal has a definite pattern of attachment to body wall by muscular mesenteries, differing in minor details in the three species (pl. 35, fig. 1). The slender foregut is very extensive, consisting of pharynx, esophagus, crop (subtended by a powerful muscular mesentery not attached to body), a long gizzard, and a stomach attached posteriorly by a strong mesentery. The greater part of the very long midgut is accompanied by the siphon, which starts close to distal end of stomach. The ciliated groove of midgut, which parallels the siphon, extends beyond it to the point where the gut is suddenly expanded into the inflatable respiratory portion. The external ridge marking the ciliated groove continues along dorsal side of this expansion, passing distally to the right where it affords attachment for mesenteries, but there is no groove inside corresponding to it. This inflatable so-called "hind-gut" is equivalent to the terminal part of the midgut of *Echiurus* (which is not enlarged). The only similar abrupt enlargement occurs in *Nellobia eusoma.* The true hind-gut or cloacal cavity is separated from the foregoing by a definite sphincter constriction and consists of a thin-walled anterior portion and a thicker-walled terminal section with rugose mucosa. Very numerous frenula attach cloaca to body wall and account for the expansion of cavity by which water is inhaled during respiration. The anal vesicles are voluminous, slender sacs, always deflated, which open ventrally into terminal portion of cloaca. The glandular walls are externally rather cauliflowerlike and the entire inner surface is intricately plicated. The scattered ciliated funnels are very tiny. The anus is eccentric to the circle of setae, being slightly nearer the ventral side (pl. 33, fig. 4).

670329—46——4

Remarks.—Three well-known species have a very uniform outer facies. Although *unicinctus* of Japan has only two pairs of nephridia, it is indistinguishable by external features from small examples of *caupo*. The details of skin and setae are practically identical. The alimentary canal, except for minor details of mesenteries, is closely similar in the two species. Apparently *unicinctus* does not reach the large size of *caupo* and *chilensis*, both of which have a third (posterior) pair of nephridia. The anterior setae of *chilensis* are blunt and scarcely tapered while in the other two species they are strongly tapered and sharp. In *chilensis*, as compared to *caupo*, dorsoventral muscle *13* is weaker, the crop and gizzard are longer, and the interval between end of stomach and beginning of siphon is about three times greater. The attachment of the anterior end of the respiratory portion of midgut (pl. 36, figs. 1, 2) presents important differences.

Urechis chilensis (Müller), synonym *U. farcimen* (Baird), is found at Sandy Point, Strait of Magellan. My specimen, taken by the Hassler Expedition, was kindly donated by the Museum of Comparative Zoology.

A fourth species, *Urechis novae-zelandiae* (Dendy), awaits detailed investigation (Dendy, 1898; Poche, 1920).

Dr. Carlos E. Porter, of Santiago, Chile, has called attention (*in litt.*) to the name *Pinuca edulis* Claudio Gay (1854, p. 475). Dr. W. L. Schmitt, to whom Dr. Porter sent the information, had photographs made of the five pages covering the section on "Sipunculides" in the "Historia . . . de Chile." Four of these are pages 53–56 of volume 3 published in 1849 and list *Sipunculus lagena* and *S. cylindricus*. *Pinuca edulis* is described in supplementary volume 8, published in 1854, as follows:

> Añade tomo III, pág 56. *Pinuca edulis.* Por haber perdido los ejemplares que teniamos de este singular Sipunculiano, es preciso á lo menos señalarlo á la atencion de los naturalistas y viajeros. Segun nuestro diario es de un blanco pardusco súcio y tiene de dos á tres pulgadas de largo y como una de ancho. Su cuerpo es subcilíndrico, ligeramente hinchado en el medio y adelgazado en ambas puntas, siendo la anterior mucho mas obtusa que la posterior. El cuero es grueso, coriáceo, un tanto arrugado en al traves, ló que proviene de la reunion de una infinidad de pentitos mas ó menos prominentes. La boca es pequeña, arugada, rodeada, á poca distancia, de muy pequeños aguijones apenas visibles, subretractiles y dispuestos en círculo. El ano se halla á la otra extremidad y es bastante grande, liso, círcular y un poco hendido. Un diseño hecho en el lugar, señala hácia el medio una reunion de pequeños cuerpos dispuestos en una banda círcular de una línea poco mas ó menos de ancho.
>
> Este animal que los habitantes comen cocido en la brasa despues de haberle quitado las dos extremidades, se halla en las arenas de la isla de Chiloe cerca de Castro, etc. En mi diario hallo notado que hace el pasaje de los Priapos á los Sipúnculos.

Without specimens from Chiloé Island it is not possible to determine whether *Pinuca edulis* is the same animal as *Urechis chilensis*, which has not been reported so far north. If *Pinuca* is an *Urechis* it is

obvious that Gay has the mouth and anus confused; and the length of 2 or 3 inches is small for the average size. There are other discrepancies. In a *Urechis* 3 inches long, the anal setae are not "scarcely visible" but are conspicuous; no mention is made of the prominent anterior setae; no specimen of *Urechis* displays "hácia el medio una reunion de pequeños cuerpos dispuestos en una banda círcular de una línea poco ó menos de ancho," whether "medio" refers to the body or to the anus (mouth), which just precedes this sentence in the description.

The curious respiratory mechanism of *Urechis*, in connection with the loss of its blood vessels and the complexity of its blood physiology, relegates the genus to a very isolated position. Not less important is the behavior pattern whereby the requirements of respiration and food are beautifully met and coordinated. At every point specialization of habit is matched by structural and physiological adjustment of the most delicate and efficient description. Along with this specialization and complexity is an amazing viability best expressed by the term "tough."[23]

All signs point to *Urechis* as being the last of a very ancient stock, one that may have flowered into many species during Paleozoic times. It belongs to the honorable company of *Lingula* and those other aristocrats sometimes referred to as "living fossils."

URECHIS CAUPO Fisher and MacGinitie

FIGURES 17–19; PLATES 33–35; PLATE 36, FIGURES 2, 4; PLATE 37

Echiurus sp. JOHNSON and SNOOK, 1927, p. 178, fig. 153.
Urechis caupo FISHER and MACGINITIE, 1928a, p. 200, pl. 9, figs. 1–6; 1928b, p. 204, figs. 1–3, pl. 10.—BAUMBERGER and MICHAELIS, 1931, p. 417.—REDFIELD and FLORKIN, 1931, p. 185.—HALL, 1931, p. 400.—SATO, 1931, p. 178.—NEWBY, 1932, p. 387; 1940; 1941, p. 303.—MACGINITIE, 1935a, p. 341; 1935b, p. 602; 1935c, p. 483; 1938, p. 208.

Description.—The species reaches a large size. One specimen collected by G. E. MacGinitie at Humboldt Bay, Calif., measures 470 mm. long by 55 mm. thick. The largest specimen from Elkhorn Slough, Monterey Bay, Calif., was 500 mm. long when fully relaxed in anesthesia, but after preservation it shrank to 375 mm. in length by 35 mm. in diameter. These were undoubtedly very old individuals. Average specimens are 150 to 180 mm. long.

The surface of the body is traversed by fine irregular channels giving a rugose appearance, which is most pronounced in the head region anterior to the zone of slime glands. The latter, a sort of clitellum, is usually distinguishable by the circular trend of its fine furrows. Its anterior border coincides roughly with the second pair of nephridia,

[23] See Redfield and Florkin, 1931; Baumberger and Michaelis, 1931; Hall, 1931; MacGinitie, 1935a, 1935c; Newby, 1940, 1941; Fisher and MacGinitie, 1928a.

while the posterior border is spaced behind the third pair a distance about equal to interval between second and third pairs. This zone contains the slime-net glands. "Three to 10 or even more glands are located on the outer surface and in the outer part of the sides of the papillae. These glands develop from the surface epithelium and are formed by an invagination of this layer of cells and the outlying cuticle. The gland cells develop numerous terminal cones which penetrate into the cuticle of the duct (formed by invagination). During the secretion of any one slime-net only about one-eighth of the gland cells are active. In these cells the terminal cones perforate the cuticle and open into the duct as minute tubules from which the fibrous secretion which forms the slime-net is discharged. The net

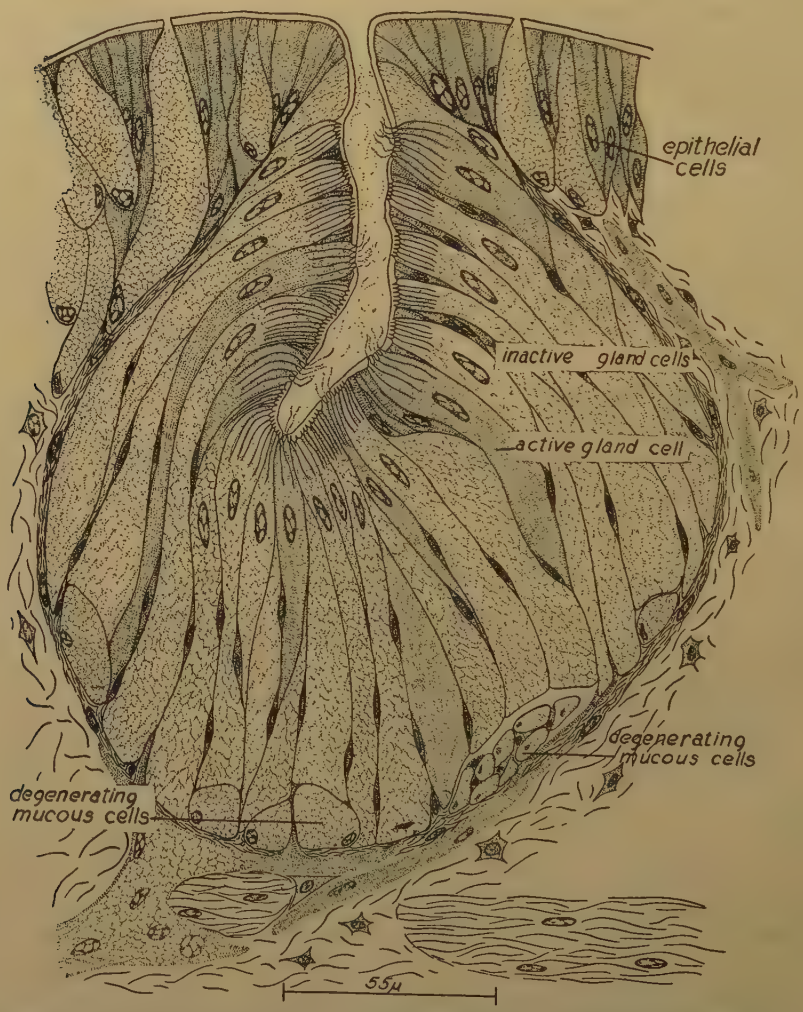

FIGURE 17.—*Urechis caupo* Fisher and MacGintie: A vertical section of a mature slime-net gland taken while actively secreting; drawing by W. W. Newby (1941).

itself is probably fibrous in nature, although this has not been demonstrated. [Figs. 17, 18.]

"The body wall consists of the cuticle, the surface epithelium or epidermis, and the underlying connective tissue called the cutis (Jameson, 1899, p. 572) or corium (Seitz, 1907, p. 326). These three layers constitute the skin. Beneath them are the outer circular, the longitudinal, the inner circular muscle layers and the parietal peritoneum." [24]

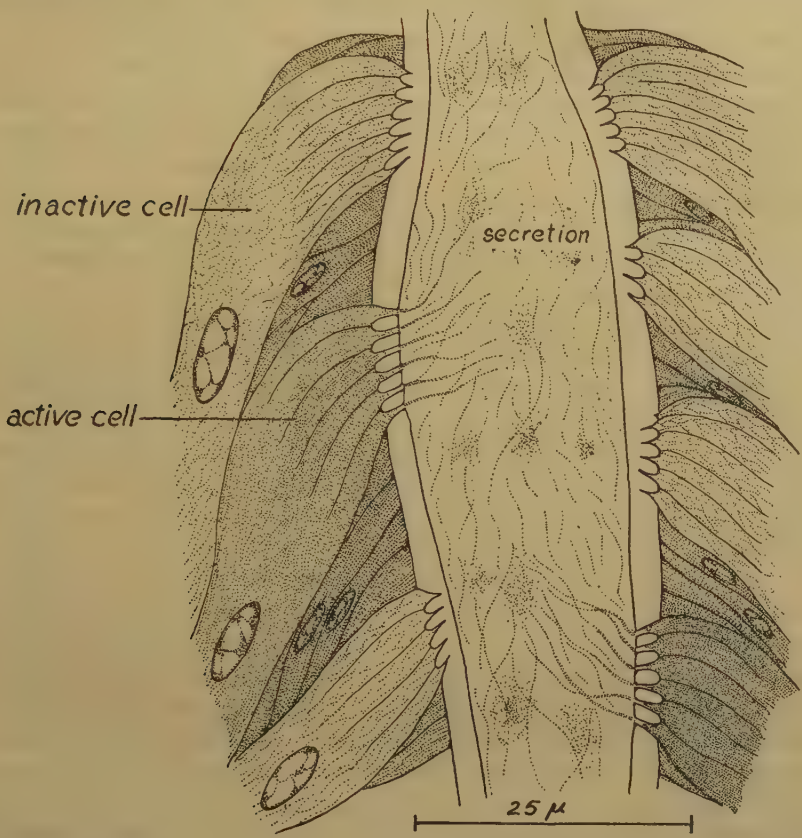

FIGURE 18.—*Urechis caupo* Fisher and MacGinitie: A vertical section of the middle part of a slime-net gland taken while actively secreting; drawing by W. W. Newby (1941).

Anterior setae terminally tapered, sharp, curved, situated, in large specimens, 3 to 5 mm. back of the groove leading to mouth and about the same distance apart. They are metallic yellow, brownish at tip, 8.5 to 10.5 mm. long. The flattened, curved exserted portion is more tapered and sharper than in *chilensis*. A strong interbasal muscle is

[24] Newby, 1941, pp. 304, 315; figs. 1–10. Dr. Newby has subjected the slime glands to a thorough histological study. He has kindly contributed the original drawings of figures 17 and 18, which are from the above paper.

present, and numerous somewhat variable muscles radiate from the coelomic end. Inside the seta sac a short substitute seta is often present close beside the functional one.

Anal setae curved terminally, sharp, 10 or 11 in number, and the dorsal are longer (8.5 mm.) than the ventral (7.3 mm.). The dorsal are the only ones used to any extent in cleaning out the burrow. When digging, the posterior end of the body is bent sharply forward, underneath, so that the ventral setae touch the ventral surface of the worm, while the strongly exserted dorsal bristles scrape the mud backward as the body is again straightened. This habit helps to explain the absence of a midventral seta, there being a broader gap at that point. The anus is eccentric to the circle of setae, being nearer to the ventral side (center of anus 6 or 6.5 mm. from dorsal setae and 4 or 4.5 mm. from the ventral). All bristles show conspicuous cross-banding.

There are three pairs of nephridia varying greatly in size according to degree of distension with eggs or sperm. In one specimen examined the posterior tubes were 150 mm. long and 10 mm. in diameter, reaching two-thirds the total length of animal. The anterior pair is situated close to the setae. Rarely, one nephridium of this pair is missing. The nephrostome is on the anterior side at the base and the grooved ciliated lips are very long and spirally coiled. MacGinitie (1935a) has shown that the superficial groove, V-shape in section in the male and more C-shape in the female, communicates by a slit along its bottom with what is virtually an almost closed duct or tube underneath. In both upper and deeper parts of groove the cilia beat toward the nephridium while on the outside of the lips, bordering the superficial groove, they carry materials in the opposite direction and incidentally help in the circulation of the coelomic fluid and contained blood cells. "As the eggs, blood cells, and other coelomic materials pass along the outside of the thread the eggs are caught in the external portion of the groove, are fed into the inner channel and then proceed to the opening leading into the storage reservoir [nephridium]. They are carried toward the reservoir at the approximate rate of 7 spirals per minute. Thus the eggs are separated from all other coelomic materials. As the eggs pass through the slit between the external portion of the groove to the inner channel, they are under considerable pressure. They enter as a wedge, then become disc-shaped in the slit, and finally round out in the inner channel. Only mature eggs with indentations are collected in this way. As the eggs pass along the inner groove toward the storage organ they become oriented with the convex surface of one egg pushed into the indentation of the egg ahead, thus forming a compact chain. Blood cells (which range from 0.014 to 0.02 mm. in diameter) and immature egg cells pass along the collecting threads (i. e.,

the spiral lips) without lodging in the external groove. Sperm is collected in the outer groove of male collecting threads, fed into the inner groove, and carried to the storage organ." [25]

There is no permanent gonad. "Sex cells in all stages of development, from very immature ones to those which appear to be fully mature are found in the coelomic fluid at all times of the year. In the case of the male, the apparently mature, free-floating sex cells are known to be functional." (MacGinitie, 1935c, p. 485.) "I have examined a male collected in winter as well as several specimens of both sexes collected in the summer and in these I could establish neither qualitative nor quantitative differences in the sex cells at the two seasons. Furthermore, in neither season did I find mitotic figures in any area of the peritoneum nor could I establish any evidence of division by any of the cells which were free in the coelom. Thus there is no evidence in regard to the origin of the sex cells in Urechis." (Newby, 1940, p. 7.)

MacGinitie (1935a, p. 342) estimates that there are nearly 3 billion sperms present in the nephridia of an average-sized male and over 6 million eggs in an equal-sized female. The eggs are 0.115 to 0.12 mm. in diameter according to MacGinitie (southern California specimens). C. V. Taylor measured 303 from the Monterey Bay region and found them to range between 0.123 and 0.144 mm. in diameter.[26] The egg is very clear, with a large nucleus, containing a nucleolus 0.012 to 0.016 mm. in diameter.

The anal vesicles, contracted, have a cauliflower surface beset with minute ciliated funnels. They empty, ventrally, into the posterior part of the cloaca.

In addition to abundant sex cells, the coelomic fluid is filled with nucleated red or brown blood corpuscles subcircular in shape and upward of 0.035 mm. in diameter, together with very numerous amoeboid cells, yellowish when aggregated. "The color of the blood varies from the purest oxyhemoglobin red to the darkest brown-black or a blacklike Chinese ink, even after complete saturation with oxygen. The red color is due to hemoglobin homogeneously distributed within the blood cells. Whenever the color is brown, besides this hemoglobin there is another granular pigment of brown color within the cells which will be proved to be hematin. Red blood was encountered in some few of the smallest individuals and in some of the very largest sex-mature females. The majority of the individuals, of medium size, contained brown or brown-black blood." (Baumberger and Michaelis, 1931, p. 417.)

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[25] MacGinitie, 1935a, p. 346. A careful paper based upon observation of living material and the only one describing the behavior of the nephridial appendages.

[26] Physiological Zoology, vol. 4, p. 430, 1931.

ALIMENTARY CANAL.[27]—As indicated in the family and generic diagnoses, the most characteristic features of the alimentary tract are the extremely long presiphonal foregut, with its very extended gizzard segment, and the "hind-gut" modified to act as a respiratory organ. These features are closely similar in the three species, all of which I have dissected. The apparent differences in the published figures are due to limitations of material or faulty observation. In plate 34, figure 1, the greater part of the siphonal and part of the postsiphonal gut have been removed. A very contracted specimen was used owing to limitations of plate. Here it is obvious that the foregut is considerably longer than the body. In a well-expanded preserved specimen, 300 mm. long, the pharynx is 30 mm. long; esophagus 40 mm.; crop 85 mm.; gizzard 85 mm.; stomach 50 mm.; total 310 mm. In an expanded specimen the distance between the position of the stomach and anus may equal nearly one-third body length and the muscular mesentery may be, as in the specimen under discussion, 35 mm. long. The posterior attachment of this mesentery is indicated also in plate 36, figure 4, M^2.

The pharyngeal lining is thrown into very coarse longitudinal folds, which really begin on the ventral side of proboscis and run directly to the esophagus, diminishing in size. In the esophagus the much smaller ridges are cross cut by deep narrow channels, which divide them into rings of oblong verrucae, giving the exterior a ringed appearance. The esophagus is definitely begun at the last of the dorsolateral mesenteries of pharynx (pl. 34, fig. 2, *15*). In this figure an attempt is made to show the muscular mesenteries of the pharynx by a view looking forward into the head region from just back of the first pair of nephridia. The pharynx has been pulled upward by the contraction of these dorsal and dorsolateral mesenteries *1–7* (left side). The ventral mesenteries (*14*) are the least variable. Muscle *13* (paired) is not connected with the alimentary canal but is attached below to body wall in front of the seta, and above, dorsolaterally. All these muscular mesenteries are characteristic of the genus and on direct comparison appear to be more robust in *chilensis* except *13*, which is better developed in *caupo*.

The crop (crop 1 of Seitz) is subtended by a strongly muscular mesentery not attached to body wall. The posterior part of esophagus (pl. 34, fig. 1, *X*) loses its ringed appearance, the mucosa having deep, fine, longitudinal folds. In the crop the mucosa is again regularly verrucose, but of finer texture than in esophagus. In the gizzard the mucosa is thrown into strong ring folds, formed by the annulate muscles of gizzard wall, conspicuous superficially. The

[27] Embleton, 1900, pl. 8, gives some figures of the histology of alimentary canal of *U. unicinctus;* Seitz, 1907, pl. 31, for *U. chilensis*.

crop and gizzard of *chilensis* by direct comparison are definitely longer than in *caupo* by about 25 percent.

The stomach (crop 2 of Seitz) corresponds to that of *Thalassema*, and the mucosa has about 12 distinct longiseries of compressed verrucae. Externally the stomach has the longitudinal zonation characteristic of *Thalassema* and allies. It ends abruptly at the beginning of the much wider midgut with its ciliated groove. About 3 mm. from end of stomach the siphon begins, while the ciliated groove continues adjacent to it, along the inside of intestine (pl. 35, fig. 5). A strong muscular mesentery subtends the stomach and is attached posteriorly a little to left of nerve cord (M^2). In *chilensis* the siphon begins 9 mm. from end of stomach as compared to 2.5–3 mm. in *caupo*.

The course of the intestine in a fully expanded specimen is shown in plate 35, figure 1. The anterior and posterior portions of the body are omitted. Plate 36, figure 4, shows the cloacal region of the same specimen. It will be seen that the siphonal part of the intestine is very long and includes two anterior and two posterior bends. Three segments of the gut are attached by muscular mesenteries on the right side of body and three (including the big "hind-gut") are attached on the left side. The foregut is not attached to body wall except by the strong pharnygeal mesenteries and the mesentery of the stomach (M^2). In this figure the breadth is accentuated because the body wall is pinned out flat. The mesenteries of siphonal gut farthest to right are attached about halfway between midventral and middorsal lines.

The postsiphonal "small intestine" is rather short and is anchored by heavier mesenteries than are found on the siphonal portion anterior to the last loop. The "hind-gut," used as a respiratory organ, varies in dilation and consequent thickness of wall in different specimens. The wall is usually thin and translucent. It is firmly anchored along its entire length on the left side of the nerve cord. On plate 36, figures 1–3, I have shown the attachment of the anterior end of the "hind-gut" in the three species. Unless the single specimen of *chilensis* available for dissection is abnormal, there is considerable difference between it and *caupo*.

The cloaca is probably normally elongate as shown in plate 36, figure 4. It is here shown opened for the entire length. The mucosa of the posterior third is deeply furrowed longitudinally, and in this part, on the ventral side, are the openings of the two anal vesicles. The fecal pellets which sometimes crowd the portion of small intestine shown in plate 34, figure 1, are cylindrical with rounded ends (pl. 35, fig. 6).

The fresh colors of the viscera in an anesthetized specimen are: Foregut, pale flesh or skin color; anterior third of midgut pale gray-green mottled with brown; middle third, mottled yellow and dull

gray-green; posterior third pale gray-green; siphon, pale jade green; respiratory gut, translucent raw sienna.

Type.—U.S.N.M. No. 19616.

Type locality.—Elkhorn Slough, an estuary of Monterey Bay, Calif.; shallow water, muddy sand.

Distribution.—CALIFORNIA: Humboldt Bay, Tomales Bay, Monterey Bay (see note below), Morro Bay, Newport Bay. With one exception all specimens have been found living under essentially estuarial conditions; that is, in quiet bays or sloughs in sandy mud. As a rule the openings of the burrows are under water at low tide, but are sometimes uncovered. However, in June 1923 I found one good-sized specimen in a bucket holding flounders and other fish caught in essentially open sea conditions near the Hopkins Marine Station, Pacific Grove, Calif. This record points to the probable occurrence of the species at moderate depths almost anywhere off the coast of California where mud of the proper consistency for permanent tunnels is present.[28]

History.—The first specimens of which I have any knowledge were collected in 1903 by C. S. Thompson, at Morro Bay, Calif., and brought to Stanford University. Some of these, in a good state of preservation, are still in the museum there. In 1920 I found one specimen in Elkhorn Slough, Monterey Bay, where a few years later Dr. Myrtle Johnson collected the examples from which the figures in "Seashore Animals of the Pacific Coast" were drawn. In 1923 a specimen was brought in by flounder fishermen from the sea bottom off the Hopkins Marine Station. It was not until 1926 and 1927, however, that the animal was studied. In connection with an ecological exploration of Elkhorn Slough, Prof. G. E. MacGinitie, then a graduate student working at the Hopkins Marine Station, found them in quantity. By means of narrow aquaria filled with mud ("limoria") and glass-tube facsimiles of the actual burrows, he was able to observe living animals under essentially normal conditions, for *Urechis* seems to be insensible to light. Every important fact in the ecology of *Urechis* has been discovered by Professor MacGinitie.[29]

Habitat.—The first field studies were made at Elkhorn Slough, a shallow estuary, tributary to Monterey Bay, where the water, although slightly warmer than that of the ocean (which here varies from 49° to 57° F.), has practically the same salinity, there being usually a free interchange with each tide. In this inlet dwell a considerable variety of bivalves, some of which are much sought for food. There are two very interesting decapods, *Callianassa californiensis* Dana and *Upogebia pugettensis* (Dana), which, like *Urechis*, construct

[28] Dr. Earle H. Myers tells me he has found *Urechis* in the stomach of dogfish caught northwest of San Francisco Bay entrance (Golden Gate).

[29] Fisher and MacGinitie, 1928b; MacGinitie, 1935b, pp. 682–686, 688, 715, 717; 1938, p. 208.

tunnels in the mud and conduct a more or less permanent ménage. The mud teems with annelids such as *Lumbrinereis*, and there are literally acres that have a greenish tinge from the tentacles of *Phoronopsis viridis* Hilton. *Zostera* grows in permanent patches and supports a characteristic association of animals. At favorable times wide expanses support a growth of green *Enteromorpha* which, either fresh or decayed, is an important food element, since the bulk of animal life consists of detritus feeders.

At low water broad areas are left bare, but *Urechis* usually excavates its home where the entrances are not exposed at lowest tide. A few places were found where they are exposed at lowest tide.

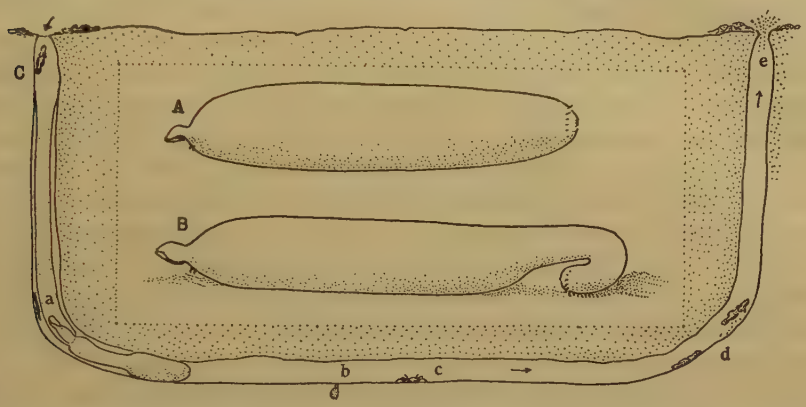

FIGURE 19.—A, *Urechis caupo* Fisher and MacGinitie, in resting posture. B, Position assumed while digging with anal setae. C, Plan of *Urechis* tunnel, the worm *in situ* pumping water through the slime-tube. Water enters at *C*, where there are two *Clevelandia ios* (one outside); at *a*, *Hespernoë* lies in wait to feed on tube when it shall be swallowed; *b*, the tiny clam *Cryptomya californica; c*, *Scleroplax; d*, *Clevelandia* creating disturbance; *e*, eruption of mud cloud on ventilating current; castings around exit.

The tunnel (fig. 19, C), never carried very deep, has two entrances and is in the form of a widely expanded U, of which the uprights are nearly perpendicular and the bottom horizontal. The apertures are small, being about one-third the diameter of the tunnel itself. Around one of the openings there is a considerable quantity of castings. The greatest distance between entrances measured 38 inches, the shortest 16 inches. Twenty-seven was the average for many measurements. The distance apart of the two entrances depends upon the size of the animal but not proportionately so, for small specimens have more extensive burrows for their size than larger ones. The largest specimen obtained was 19.5 inches long when relaxed in anesthesia, and the smallest was 1 inch.

The burrows have a permanent aspect and none of those continually observed was found changed except that occasionally one had a new entrance. The animals grow very slowly, and so the enlargements need

be made only at infrequent intervals and then only by widening the U and extending one of the entrances.

Locomotion.—A *Urechis* can move along a smooth surface in much the same manner as an earthworm. It elongates the anterior part of the body and then forces forward the viscera and the water contained in the respiratory gut by contracting the posterior region and relaxing the anterior. When most of the body weight is in the anterior end the posterior portion is drawn up. These movements are repeated as the animal proceeds. Its method of locomotion within the burrow is quite similar except that the animal has the added advantage of being able to wedge the anterior portion against the sides of the burrow. Its rapidity of locomotion approximates that of an earthworm. It can move considerably faster when in the burrow than when out of it, and it can move backward nearly as fast as forward.

Digging.—When digging a tunnel *Urechis* forces its proboscis into the mud and works out a hole until the body can be drawn into it. This process is continued until the worm completes a U-shaped tunnel open to the surface at both ends, so that a supply of fresh water may be pumped through the tube by peristaltic movements of the body. Then the bore of the tunnel is enlarged by scraping material from the sides by means of the anterior setae, working it backward with the anal setae, and finally blowing it out the "back door" by a blast of accumulated respiration water from the hind-gut. To loosen sand from the sides of the burrow, the oral setae are protruded, then drawn backward through the sandy mud. This digging is done on all sides of the burrow as the animal can rotate its body at will. The setae are shed occasionally and renewed.

The use of the anal setae, which form a ring of 10 or 11 a short distance from the anus, is highly characteristic and was carefully observed. The sharp retractile bristles curve forward. The mid-ventral seta is lacking, and the pair on each side are distinctly shorter than the four or five dorsal setae. When a certain amount of loosened debris accumulates from the activities of the anterior bristles, *Urechis* crawls over it and forces it backward, in one of two ways: either by blowing the sand along with anal-water jets, augmented by the vigorous ventilating stream of the tube, or by turning under the posterior end of the body and then vigorously straightening it (fig. 19, B). The loosened material is shoved along the tunnel, whereupon the anal jet and ventilation current propel the finer detritus still farther. The animal backs up and repeats the process. When the posterior end is folded under, the dorsal setae are strongly everted and their forward curvature favors efficient scraping. The ventral setae (now dorsal in position) are against the ventral body wall and do not function. A reason for the smaller ventral setae (and the absence of the mid-

ventral seta) is now apparent, if we have faith in the efficacy of use and nonuse in determining the relative size of similar organs.

Castings are sometimes ejected from the burrow by this flipping of the posterior end of the body (which can be admirably imitated with the forefinger), but usually only by water currents. Castings are allowed to accumulate and then are ejected in quantity from one entrance. When digging downhill the animal shoves the soil along the body and then out by backing up the burrow, forcing the sand out the last inch or two by water currents. The opening then resembles a miniature volcano with fine dark sand spouting out and the roily water trailing off from the crater like smoke. A major convulsion will carry out fragments of shells 2 or 3 mm. in section. Larger objects are avoided or allowed to fall toward the lower part of the burrow where they are buried. Doubling the velocity of water increases its carrying efficiency directly as the sixth power. The narrowed mouth of the tunnel undoubtedly aids in increasing the force of these "volcanic" manifestations and hence their efficiency in removing sizable debris.

Once *Urechis* is settled in a permanent home its daily activities consist of respiratory movements, obtaining food, cleaning the burrow, and resting.

Respiratory movements.—There are two separate movements concerned with the respiration of *Urechis:* (1) The peristaltic movements along the body which pump fresh water into the tunnel and move that within respiratory chamber of the intestine; (2) the inhalations and exhalations, through the anus, for which the muscular cloacal chamber, resembling that of a holothurian, supplies the chief motive power.

The inhalations are from 1 to upward of 30 in succession (without an exhalation). Exhalation is usually a single discharge although infrequently a rest may occur during a period of exhalation. The rate of breathing is not uniform. For instance, 2 inspirations covering 25 seconds were followed by an expiration period of 10 seconds, while in another instance 7 inspirations occupied 25 seconds, the expiration 10; 24 inspirations occupied 70 seconds, the single expiration 50; 30 inspirations occupied 90 seconds, the expirations only 25. Inspirations fewer than 12 predominate in a total of 11 cycles timed. These times were taken on a specimen lying in a pan of water. In its natural environment *Urechis* breathes more slowly, but with the same irregularity.

The peristaltic movements of the body which serve to propel water through the tube are even more erratic. The wave, which expands the body to fill the burrow, begins at the base of the proboscis and passes along the body at varying rates for different waves or even the same wave in different parts of the body. As one wave arrives at the

posterior portion of the body a new one begins at the anterior end. *Urechis* is normally always in control of the water and senses anything which may attempt to pass through the burrow.

Feeding.—The unique method employed by *Urechis* to gather nourishment is generic and furnishes a striking example of the coordination of adaptive structure and behavior.

A short distance back of the oral setae is a zone of compound mucous glands, which form a sort of clitellum very faintly differentiated externally by the ringlike arrangement of the low rugosities of the skin. These glands are specializations of the simpler and more numerous multicellular flask-form mucous glands of the integument. The slime-net or girdle glands, as they have been called, secrete a fairly long transparent mucous tube, or funnel, whose upper, open end is fastened near the mouth of the tunnel while the lower remains attached to the clitellum. This strains from the ventilating, or respiratory currents, all minute particles as the water flows through and when sufficiently loaded the tube is swallowed. The process is repeated as long as the animal feeds. *Urechis* readily adopts a glass substitute for its normal burrow so that feeding reactions can be closely followed (pl. 37, fig. 1).

Just before starting a tube, the body is constricted at the clitellum. This region is then expanded until it presses firmly against the sides of the burrow (usually near the mouth, but sometimes in the horizontal portion) with which it remains in contact for about 2 seconds. During the spinning process, which occupies only a few minutes, the constricted portion of the body anterior to the clitellum (whence the slime is issuing) undergoes a curious spiral peristalsis (pl. 37, fig. 5) easily detected by watching the nerve cord, which shows through the pink body wall, while back of the clitellum the normal respiratory, or pumping, peristalsis is taking place.

The tubes vary in length from about 2 to 8 inches without apparent reason. As the tube lengthens *Urechis* backs down the tunnel, and on completion the spiral peristalsis anterior to the clitellum ceases, being replaced by a faint normal peristalsis, the main wave starting just back of the attachment of slime tube to the body. These normal ventilating reactions are kept up until the animal, apparently sensing the blocking of the water current by the clogging of the mucus with detritus, slips the tube forward "over its head." In doing this it deftly catches the hind edge of the tube by expanding the proboscis and bending it backward, collarwise, against the inflated nuchal region, until the muscular pharynx is able to pick up and suck in a portion of the margin (pl. 37, fig. 7). When diatom culture or detritus is introduced with a pipette the slime tube is soon swallowed; but if unmolested, *Urechis* may continue pumping for an hour before the tube is clogged.

Usually only a few minutes are required for swallowing the tube, but the time depends upon length of tube and the amount of detritus intercepted. When the tube has been swallowed up to the point of attachment the animal makes a movement to release it from the sides of the burrow similar to the reaction while digging with oral setae.

The food funnel is porous to liquid but will intercept the smallest particles. Phenol red passes through everywhere, but no carmine particles ever do. Under the microscope no openings can be detected, but particles approaching a micron in diameter are lodged in the mucus.

When first secreted the tube is perfectly transparent, but as it collects detritus it becomes gray and its outlines are easily seen. Peristalsis becomes more energetic as the tube-wall fills.

When spinning the tube or lying at its lower end pumping water through it, *Urechis* is very sensitive to disturbances. If water is injected into the mouth of the tunnel, the animal immediately ceases movement and remains perfectly still for a minute, then slowly resumes peristalsis. If the disturbance is too great, it will drop out of the tube and retreat toward the center of the burrow, returning later to eat the slime tube. While it is lying at the end of a completed slime tube any slight disturbance such as the introduction of a little mud or fresh clean meat will cause *Urechis* at once to pass the tube forward and begin swallowing. No large particles are ingested. They are rejected as the tube is being swallowed.

Urechis feeds to some extent, although not very efficiently, when lying without its burrow in an aquarium. In such a position it will swallow sediment from the bottom of the aquarium gathering it with the proboscis.

Resting.—After a period of feeding *Urechis* goes to the horizontal portion of the burrow, contracts its body so that it fits the tunnel snugly, and lies in a state of suspended activity during which even respiration ceases. These rests may last for an hour or more, but the long rests are always preceded by one or more short rests, which last 4 to 8 minutes, and between which respiratory water is expelled and more taken in (fig. 19, A).

Commensals (pl. 37, figs. 1–3).—*Urechis* has three permanent commensals: A polynoid annelid, *Hesperonoë adventor* (Skogsberg), and 2 pinnotherid crabs, *Scleroplax granulata* Rathbun and *Pinnixa franciscana* Rathbun. Sometimes all three are found in the same burrow, but usually only a *Hesperonoë* and either a *Scleroplax* or a *Pinnixa*. In addition, the little *Cryptomya californica* (Conrad) projects its siphons into the burrow to make use of the water in the burrow for its source of food and oxygen. The goby *Clevelandia ios* (Jordan and Gilbert) uses the burrow as a retreat rather than a residence, as the little fish freely forages outside, returning when alarmed

or when the entrance is left exposed by low tide. On such occasions one to five gobies may be taken from the upper part of the tunnel. A goby left at the laboratory for several weeks in a glass burrow appeared contented. It would pass from one end to the other, wriggling past the *Urechis* as if accustomed to doing so. At Newport Bay a pair of either *Betaeus longidactylus* Lockington or *Crangon* [*Alphaeus*] *californiensis* (Holmes) have been found permanently established in the burrows of *Urechis*. The former is also recorded from Elkhorn Slough from *Urechis* burrows (MacGinitie, 1935b, p. 706).

Hesperonoë adventor, which ranges in length when alive from 15 to 50 mm., is commensal with *Urechis* throughout its range from Humboldt Bay to Newport Bay and normally is not found outside the burrows. The food of *Hesperonoë* consists of particles rejected by *Urechis* when swallowing its slime tube. These particles consist of either living or dead animals which wash down the burrow with the current and become entrapped in the slime-net. Sometimes when *Urechis* is swallowing its slime tube the polynoid will crawl forward and eat part of the tube and contents. It is very aggressive toward intruders within the burrow other than the commensal crabs. Only one *Hesperonoë* occurs within each burrow, and if another enters the two will fight until one is killed or driven from the burrow. Other annelid worms which may find their way into the burrow are speedily dispatched (by means of the short eversible toothed proboscis) and devoured.

Hesperonoë rests with its dorsal surface in contact with the body of *Urechis*, moving along the burrow with the latter by making little short runs as the peristaltic movement of the body of *Urechis* passes by. It always faces in the same direction as *Urechis*, and when the latter turns in its burrow the annelid quickly does likewise. *Hesperonoë* is also commensal in *Echiurus* tunnels.

Scleroplax ranges from 3 to 13 mm. across the carapace and is commensal also in the tubes of *Callianassa californiensis* and *Upogebia pugettensis*. It rests facing the side of the burrow, the chelipeds turned up in front and the last pair of legs raised behind. In this posture it can travel sidewise along the tube much faster than its host. Its food consists of particles which wash into the burrows or are uncovered by the hosts. *Pinnixa franciscana* screens detritus by means of its second maxillipeds, and it will also feed on particles of worms, clams, etc. *Scleroplax* has never been observed screening plankton. As many as six *Scleroplax* have been taken from one *Urechis* burrow. A male and a female are often found together or two females. In one instance an ovigerous female was found with an ovigerous *Pinnixa*, and in another burrow a male *Scleroplax* and a male *Pinnixa*.

Enemies.—*Urechis* probably attains a ripe old age. Five specimens of different size, kept in mud in the laboratory for over a year, appear not to have grown. However, as their food is principally detritus, and as natural conditions are necessary to keep this stirred up in order that any quantity may be drawn into the slime net, laboratory growth tests are not convincing. Yet what might be termed the settled habits of the creature and the scarcity of very small specimens point strongly toward longevity. The only animal known to prey upon them is the sting ray (*Myliobatus californicus* Gill), which can dig out an occasional *Urechis*. In the ocean, however, small worms are possibly eaten by flatfishes, which regularly feed upon *Listriolobus pelodes*. As already noted, Dr. Earle H. Myers found *Urechis* in the stomach of small sharks.

The period of mortality probably comes during the larval stage. The small goby (*Clevelandia ios*) is extremely numerous, darting here and there, for any moving particles. These fish range from half an inch to 1½ inches in length and often devour objects so small as to be invisible to the observer. On one occasion 400 of these little gobies were netted from a hole, 3 by 6 feet, left by clam diggers. In addition the tiny *Urechis* must run the gauntlet of a host of small predaceous crustaceans, annelids, nemerteans, and mollusks which forage on the surface and in the upper layers of mud. Once established in a burrow *Urechis* is relatively safe.

Parasite.—I have found rather numerous cestode larvae 0.25–0.32 mm. long in the proximal end of the siphon where they perhaps cause the hernialike swellings of the siphon wall (pl. 35, figs. 4, 4a, 5). Probably the adult is to be found in the sting ray.

Spawning.—Stored sex products are found in the nephridia throughout the year. MacGinitie (1938, p. 208) states that normal spawning takes place during a short season, usually in spring or at the beginning of summer as the temperature of the water rises. One male which he kept in the laboratory for two or three years spawned on May 24 and 25. Just prior to spawning the worm came nearly to the opening of the glass tube which served as a habitation. Three welts were thrown around the body so that the circular creases were just anterior to each of the three pairs of gonopores, and the gonopores themselves were somewhat protruded and turned toward the anterior end of the body, and, therefore, toward the opening of the tube. The gonopores became quite conspicuous; this was followed by several retching movements, as if the animal were attempting to regurgitate, and then sperm issued in a stream from each gonopore. When the sperm ceased to be expelled, the animal underwent violent peristalsis, the waves running from the posterior to the anterior end, causing the sperm to pour out of the glass tube. The retching, followed by the violent antiperistalsis, was performed three distinct times. On both days after spawning the

worm went back to the bottom of the tube, pumped vigorously for some time, and then resumed feeding. During spawning the body of the worm was much more elongated than normally. The spawning on May 24 occurred at 4:30 p. m., that on the following days at 9:20 a. m. Although tne nephridia were emptied the first day of spawning, the movements and procedure on the second day were the same as for the first spawning, but very little sperm was discharged.

The embryology of *Urechis caupo*, outside the scope of this paper, has been thoroughly described and figured by Dr. W. W. Newby (1940). In this paper, which merits the highest praise, the relation of the Echiuroidea to other phyla is fully discussed.

ADDENDUM

In 1942 Dr. Sixten Bock published an important memoir "On the Structure and Affinities of '*Thalassema*' *lankesteri* Herdman and the Classification of the Group Echiuroidea." Owing to delays occasioned by the war, it has been possible to incorporate only the most important systematic data in the foregoing report, such as the new genera *Ikedosoma* and *Maxmülleria*. It is to be hoped that Dr. Bock will continue his fundamental work and will be able to revise the genus *Ochetostoma*, badly in need of an overhauling.

As Dr. Bock's scheme of classification differs from mine, it is given herewith in skeleton form:

Class ECHIUROIDEA [of phylum Annelida]
- I. Order ECHIUROINEA, nov.
  - 1. Family Echiuridae Baird, 1868. Genera: *Echiurus* and *Urechis*.
  - 2. Family Thalassematidae, nov.
    - a. Subfamily Ikedinae, nov. Genus: *Ikeda*.
    - b. Subfamily Thalassematinae, nov. Genera: *Thalassema*, *Ochetostoma* (incl. *Listriolobus*), *Ikedosoma*, *Arhynchite*.
  - 3. Family Bonelliidae Baird, 1868. Genera: *Maxmülleria*, *Acanthohamingia*, *Archibonellia*, *Hamingia*, *Parabonellia*, *Protobonellia*, *Pseudobonellia*, *Bonellia*.
- II. Order SACCOSOMATINEA, nov.
  - 1. Family Saccosomatidae Theel, 1906. Genus: *Saccosoma*.
- III. Order POEOBIINEA, nov.
  - 1. Family Poeobiidae Heath, 1930. Genus: *Poeobius*.

"The two latter orders comprise each a single species and they must be regarded as very aberrant Annelids of somewhat doubtful relationship to the true Echiuroids" (p. 17).

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EXPLANATION OF PLATES

All figures were made by the writer directly from dissections or specimens.

Plate 20

Echiurus echiurus alaskanus, new subspecies

1, Dorsal view of anatomy of anterior portion of body, × 5. Body wall is indicated only in pharyngeal region. Junction of diaphragm to body wall is indicated by dashes for dorsal half and dots for ventral half. Coiled loops of esophagus are shown emerging from posterior opening of diaphragm, below the interbasal muscle. Lines radiating from pharynx are the muscular frenula. The peripharyngeal coelom is shaded.

2, Anal bristle from posterior ring, 7.5 mm. long.

3, Anal bristle from anterior ring, 8 mm. long.

4, Diagram of the diaphragm (ventral half dotted) showing the posterodorsal opening. The esophagus is omitted except where it pierces the right wall and becomes the gizzard. The edges that are attached to body wall and ventral mesenteries are dashes.

5, Diagram of a section through diaphragm showing how its lower border merges with the ventral mesenteries.

B^1–B^4, dorsal, ring, neurointestinal, and ventral blood vessels, respectively; *C*, stomach; *CG*, ciliated groove; *D*, diaphragm; *G*, gizzard; *MD*, dorsa mesenteries of esophagus; *MV*, ventral mesenteries of esophagus (fig. 5); *N*, nephridium; *NC*, nerve cord; *O*, esophagus, indicated by arrows, ventral mesentery omitted, dorsal mesenteries shown as lighter lines; *P*, pharynx; *S1*, anterior end of siphon; *X*, perivisceral coelom (fig. 4); X^1, peripharyngeal coelom.

Plate 21

Listriolobus pelodes, new species

1, Ventral view of a large specimen from Monterey Bay, Calif., × 1½.

2, Same specimen, × 5, ventral view of anterior end showing nerve loop in proboscis, a section of which has been removed.

4, Small phase before muscle bands are evident, natural size.

4*a*, Side view of anterior end of a living specimen, × 3.

4*b*, A female, × 3, showing nephridia and fecal pellets. At this size the muscle bands are not apparent unless the specimen is strongly contracted. Outline from living animal.

Ochetostoma octomyotum, new species

3, Ventral view of type specimen from Newport Bay, Calif., natural size. A specimen from Cabrillo Beach, near San Pedro, 95 mm. long, has a proboscis 93 mm.

Plate 22

Listriolobus pelodes, new species

Type specimen, × 7, dissected to show organs of anterior portion of the body; the alimentary canal is drawn to the right of its natural position.

B^1, dorsal blood vessel; B^2, ring vessel; B^3, neurointestinal connective; B^4, ventral vessel; *C*, stomach; *CG*, ciliated groove of intestine; *G*, gizzard; *I*, intestine;

MI, interbasal muscle of setae; *N*, nephridium; *NC*, nerve cord; *O*, esophagus; *P*, pharynx; P^1, posterior end of pharynx; *S*, seta; *Si1*, anterior end of siphon; *VM*, ventral mesentery; *X*, parasite.

Plate 23

Ochetostoma octomyotum, new species

1, Dissection, × 2; the spiral funnels of the nephridia and longitudinal muscle bands have been omitted except the midventral, which is lighter shaded.
2, Interval between right ventrolateral and lateral muscles at middle of body showing fascicles of the oblique layer. On the lower left corner the oblique layer has been removed, × 20.
3, Cloaca and adjacent part of intestine opened to show relation with intestinal coecum and anal vesicles, × 5.

Lettering as for plate 24.

Plate 24

Ochetostoma octomyotum, new species

The anterior portion of plate 23, figure 1, enlarged × 5 and with addition of details.

A, anus; *AV*, anal vesicles; AV^1, their opening into cloaca; B^1, dorsal blood vessel; B^2, ring vessel; B^3, neurointestinal connective of which B^2 is merely a part; B^4, ventral vessel; *C*, stomach; *CF*, ciliated funnel or nephrostome; *CG*, ciliated groove of intestine; *Cl*, cloaca; *DM*, dorsal mesentery of pharynx, *G*, gizzard; *IC*, intestinal coecum; IC^1, its opening into cloaca; *MC*, outer circular muscle layer; *MD*, dorsal muscle band; *MDL*, dorsolateral muscle band; *ML*, lateral muscle band; *MO*, oblique inner layer of muscles; *MVL*, ventrolateral muscle band; *N*, nephridium; *NC*, nerve cord; *O*, esophagus; *P*, pharynx; *S*, seta; *Si*, siphon; *Si1*, entrance to siphon; *Si2*, end of siphon; *VM*, ventral mesentery of pharynx.

Plate 25

Arhynchite inamoenus, new species

1, Ventral view of paratype, × 1.
2, Seta of type, × 10.
3, Dissection of anterior complex of type, × 7, showing foregut in situ.
4, Skin of figure 1, from near midventral line, enlarged.
5, Type, × 7; the interbasal muscle has been cut and the liberated foregut drawn to the right; ventral mesentery is dotted.

B^1, B^3, B^4, dorsal, neurointestinal, and ventral blood vessels, respectively; *CF*, nephrostome; *G*, gizzard; *M*, mouth; *MI*, interbasal muscle; *N*, nephridium; *NC*, nerve cord; *O*, esophagus; *P*, pharynx; *S*, seta.

Plate 26

Bonelliopsis alaskana, new genus and species

1, Dissection of specimen from Unalaska, dorsal view, × 4.
2, Tip of one of the primary branches of an anal vesicle, showing two secondary branches with their ciliated funnels, × 50.
3, One of the ciliated funnels, × 200.
4, Nephrostome, × 10.

5, Anterior end of an individual, the short proboscis apparently in process of regeneration, × 3.

6, Ventral view of a worm life size; the second proboscis indicates about the maximum length in preserved specimens.

7, Anterior ventral portion of worm showing the contracted verrucose skin, × 10; when the skin is fully distended the verrucae disappear, the glandular thickenings then appearing as squarish patches, closely spaced.

Go, gonad; other lettering as for plate 24.

Plate 27

Bonelliopsis alaskana, new genus and species

1, Dissection of anterior end of a specimen with a right nephridium filled with eggs, × 5. A "window" has been cut in the dorsal wall of pharynx and also one in the nephridium to show the invaginated tip, within which is the nephrostome. The longitudinal ridges on inner wall of nephridium are indicated by dotted lines.

2, Same, anterior end, in contracted state, with right half removed to show relation of dorsal and ventral mesenteries to alimentary canal and ventral mesenteries to alimentary canal and nephridium, × 5. Anteriorly only a few of the frenula of pharynx indicated; back of these the transverse mesentery of figure 1 (M^1) is indicated as a black line. *DM*, dorsal mesentery, and DM^1 (dot-dash), its attachment to right wall of body (removed); *VM*, ventral mesentery, attached to lower side of intestine and mostly to left side of foregut and involving posterior part of dorsal artery (B^1). The nephridium lies in a sort of anterior cul-de-sac or egg trap. When the animal is extended the upper margin of dorsal mesentery is at a distance behind the nephridium, here shown at minimum size.

M^1, a transverse mesentery below the dorsal blood vessel;

M^2, special muscular mesentery between gizzard and stomach, not shown in figure 2; *PV*, position of pyloric valve, mentioned in text; other lettering as for plate 24.

Plate 28

Eubonellia valida, new genus and species

1, Dissection of anterior end of body from above, × 4. The foregut has been drawn to the left to show the large nephridium (*N*) with its terminal nephrostome (*CF*). Note the unusually long stomach (*C*), filled with pellets, between the gizzard (*G*) and intestine (*I*). The ventral blood vessel (B^4) and the much contracted neurointestinal vessel (B^3) have been cross-hatched. The dorsal blood vessel (B^1) is unshaded.

2, A cluster of nephric elements of an anal vesicle, × 30.

3, Type, natural size, from below.

4, A pellet from the postsiphonal intestine, × 10.

5, Male, from mouth cavity, × 50; anterior end to right; the sperm receptacle and duct shown.

Lettering as for plate 24.

Plate 29

Nellobia eusoma, new genus and species

1, Ventral view of anterior end of type showing the short truncate snout, × 5.

2, Ventral view of type, × 1.

3, Terminal portion of intestine, the cloaca, anus, and anal vesicles, × 5.
4, Branchlet of anal vesicle, × 50.

NP, nephridiopore; *Go*, posterior part of gonad with blood vessel and nerve cord underneath; *M*, mesenteries; other lettering as for plate 24.

Plate 30

Nellobia eusoma, new genus and species

1, Dissection of anterior portion of type, seen from above, × 5. The nephridium, filled with eggs (0.85 mm. in diameter) on the left, has a window cut in the wall to show the constricted duct from the egg chamber. The swollen duct leading to external opening lies under the nerve cord and ventral blood vessel.
2, Pharynx, × 5. Interior; anterior end looking toward mouth. The dorsal side has been cut open.

B^1, B^3, B^4, dorsal, neurointestinal, and ventral blood vessels, respectively; *CF*, nephrostome; *D*, peripheral portion of peripharyngeal diaphragm (the central portion adjacent to pharynx has been removed); *DM*, dorsal mesenteries; *G*, gizzard; *Go*, gonad; *M*, mesenterial sheet holding loop of pharynx-esophagus; *NC*, nerve cord; *O*, esophagus; *Si1*, beginning of siphon; *VM*, ventral mesentery of pharynx-esophagus; *X-Y*, probable extent of gizzard; at *Y* the canal was broken, and it is possible that a portion of the succeeding stomach was lost.

Plate 31

Acanthohamingia paradola, new species

1, Ventral aspect of paratype, × 1.
2, Same specimen; genital groove, extending forward from nephridiopore (*N*) and showing four males in situ, × 5 (♂, males attached to skin).
2*a*, Anterior portion of figure 2, × 15.
3, Type; genital groove in probably the normal closed state, × 5.
4, Genital groove of third specimen that has two nephridiopores (*N*), × 5.
4*a*, Nephridiopores of above, enlarged.
5, Male from genital groove of paratype (fig. 2), 1.19 mm. long, × 50.
6, Type; anal vesicles and thin-walled cloaca from above, × 3. The anus can be seen through the thin wall of the cloaca, and on the left most of the tubes spring from a rudimentary bladder.

I, intestine (missing from type); *M*, mouth; *N*, nephridiopore; *S*, spermotheca (nephridium).

Plate 32

Acanthohamingia paradola, new species

Dissection of anterior part of animal from above, × 4. Note the very long foregut ending at B^1 and the long (as compared with *Bonellia*) segment of intestine between B^1 and *Si1*.

B^1, B^3, B^4, dorsal, neurointestinal, and ventral blood vessels, respectively; *C*, portion corresponding to stomach of other bonelliids; *CF*, nephrostome; *G*, probable gizzard; *I*, intestine; *N*, nephridia; *NC*, nerve cord; *O*, esophagus; *P*, pharynx, *Pe*, pellet, × 10; *Si*, siphon; *Si1*, anterior end of siphon.

PLATE 33

Urechis caupo Fisher and MacGinitie

1, Dissection of contracted specimen from above, showing the intestine in haphazard convolutions. The principal mesenterial bands, which anchor the intestines to the body wall, are shown but not lettered. The coelomic apertures of the nephridia are recognizable by the conspicuous coiled lips. The arrow indicates point where pharynx becomes esophagus. The figures in sequence on the midgut are intended to aid in following the convolutions; *1* is at the beginning and *13* near the end. Beyond *13* the slight diverticulum of the respiratory gut is indicated.

2, Pharynx contracted and slit open along ventral side to show the straight longitudinal folds of lining, continuous with those of the proboscis. Posteriorly is shown characteristic lining of esophagus; on each side are the dorsal mesenteries. In front of these the ventral mesenteries are spread laterally since pharynx has been opened ventrally (see pl. 34, fig. 2, *14*).

3, Ventral surface of proboscis and anterior end of body.

4, Posterior end of body showing eccentric anus and circle of setae; + marks the midventral line.

5, Two views of the anterior setae. The line indicates 1 mm.

6, An anal seta, same scale as figure 5, with, below, a tip enlarged.

AS, anterior setae (accessory seta shown at side; muscles not drawn); *AV*, anal vesicles; C_1, C_2, crops 1 and 2 of Seitz, subtended by muscular bands M_1 and M_2; C_2 is the stomach; *CL*, cloaca, the posterior portion lined with heavy longitudinal ridges (arrows mark apertures of anal vesicles); *G*, gizzard, a portion of the foregut lying between C_1 and C_2, characterized by thick muscular walls and circular muscular ridges and constrictions; *HG*, respiratory gut, specialized posterior segment of midgut; M_1, M_2, muscular bands of crop and stomach (C_2); *N*, nephridium; *NC*, nerve cord; *O*, esophagus, anterior limit marked by an arrow; *P*, pharynx; *PS*, posterior or anal setae; *S*, siphon or accessory intestine; *S1*, beginning of siphon near beginning of midgut; *S2*, end of siphon; *VM*, ventral mesenteries of pharynx; *1–13*, these figures are in sequence along the midgut and are intended to aid in following the course; *13* is near the junction of midgut and its terminal specialized portion, the respiratory gut.

PLATE 34

Urechis caupo Fisher and MacGinitie

1, Dissection of contracted individual showing the generically characteristic parts of alimentary canal, most of the "small intestine" having been removed. The very long foregut consists of pharynx (anterior to *P*), esophagus (*O*), crop (C^1) with its strong muscular mesentery, gizzard (*G*), and stomach (C^2) anchored posteriorly by a strong mesentery here shown in maximum contraction. *S1* is beginning of siphon (pl. 35, fig. 5). Attachment of respiratory gut is always on left of nerve cord (*NC*). Along its dorsal surface is shown the muscle strand continued from the small intestines and serving posteriorly for attachment of a few dorsolateral mesenteries.

2, Head region of coelom looking forward from just behind first pair of nephridia (*16*) showing arrangement of muscular mesenteries of pharynx: *1–7*, dorsal and dorsolateral; *8–12*, lateral and ventrolateral; *13*, the dorsoventral muscles mentioned in text; *14*, ventral mesenteries of pharynx; *17*, nerve

cord; crossing the ventral mesenteries between the two figure *14*'s is the interbasal muscle of setae; radiating muscles of setae shown in solid black on right.

3, Anterior aspect of a nephridium of second pair showing nephrostome and elongated lips spirally coiled, × 5.

4, A nephridium from a specimen 40 mm. long, not yet sexually mature, × 20.

Plate 35

Urechis caupo Fisher and MacGinitie

1, Arrangement of intestine and mesenteries in fully expanded specimen, × ¾. Anterior and posterior portions of body have been omitted and the intestine has been spread to right and left to show attachments. Normally these lateralmost parts overlie the darker and more mesially located portions. A section has been removed from respiratory gut to show attachment of mesenteries. C^1, crop; C^2, stomach; *G*, gizzard; *HG*, respiratory gut; M^2, mesentery of stomach; *NC*, nerve cord; *Si*, siphon; *Si1* and *Si2*, anterior and posterior end of siphon.

2, Portion of midgut at *X* of figure 1, showing its highly sacculate structure; mucosa with fine anastomosing plications, transverse in direction; *Si*, siphon, × 2.

3, Postsiphonal midgut at *XX* of figure 1, × 2, showing the mucosa and longitudinal muscle band marking position of ciliated groove.

4, 4*a*, Cestode larvae from anterior end of the siphon, × 60. These larvae vary in length from 0.25 to 0.32 mm. and are free in the lumen of siphon and in the hernialike swellings, which may be caused by them (see fig. 5, above *Si1*).

5, Sagittal section, × 5, of the distal end of stomach and beginning of midgut and siphon, showing macroscopic character of mucosa; C^2, stomach; *CG*, one side only the ciliated groove; the groove is constituted by two of these finely plicated folds or ridges of the mucosa. The plications are coarser and the groove is broader in the short segment CG^1; *Si*, siphon, showing foliose mucosa. The cestode larvae were found in this portion and in the hernialike swellings shown just above *Si1*, the narrow passage connecting midgut and siphon.

6, Fecal pellets, × 3. Specimen from Monterey Bay, Calif.

Plate 36

1, *Urechis chilensis* (Müller): Anterior end of respiratory gut showing mode of attachment by muscular mesenteries, × 3. Compare with figures 2 and 3.

2, *Urechis caupo* Fisher and MacGinitie, × 1.5.

3, *Urechis unicinctus* (von Drasche), × 5.

4, *Urechis caupo:* Cloacal region of a relaxed specimen (pl. 35, fig. 1) with the posterior part of respiratory gut; dorsal wall of cloaca removed. *AV*, anal vesicle; M^2, muscular mesentery anchoring the stomach; M^3, muscular frenula of cloaca; *N*, nephridia; *NC*, nerve cord; *PS*, posterior setae.

Plate 37

Urechis caupo and Commensals

1, Portion of tunnel showing one position of worm while pumping water through its slime-net and characteristic stations of commensals, × ¾. *A*, *Clevelandia ios* (Jordan and Gilbert) at mouth of tube; *B*, *Hesperonoë adventor* (Skogsberg); *C*, *Scleroplax granulata* Rathbun; *D*, *Cryptomya californica* (Conrad). At upper point where tube is interrupted one inch has been omitted, at lower point four inches.

2, *Scleroplax granulata* Rathbun, male, × 3.
3, *Hesperonoë adventor* (Skogsberg), type × 1.
4, Specimen of *U. caupo* with slime-tube in place, with the thickening at point of attachment to body indicated. The worm is shown in characteristic pumping posture; × 3.
5, Characteristic posture while tube is being secreted; tube just begun; entrance indicated by dots; × 1½.
6, Expression of worm while swallowing slime-tube.
7, Grasping slime-tube at moment of starting to swallow. The proboscis is holding the posterior edge of tube while a portion is being sucked in on ventral side. This step occupies about three seconds.

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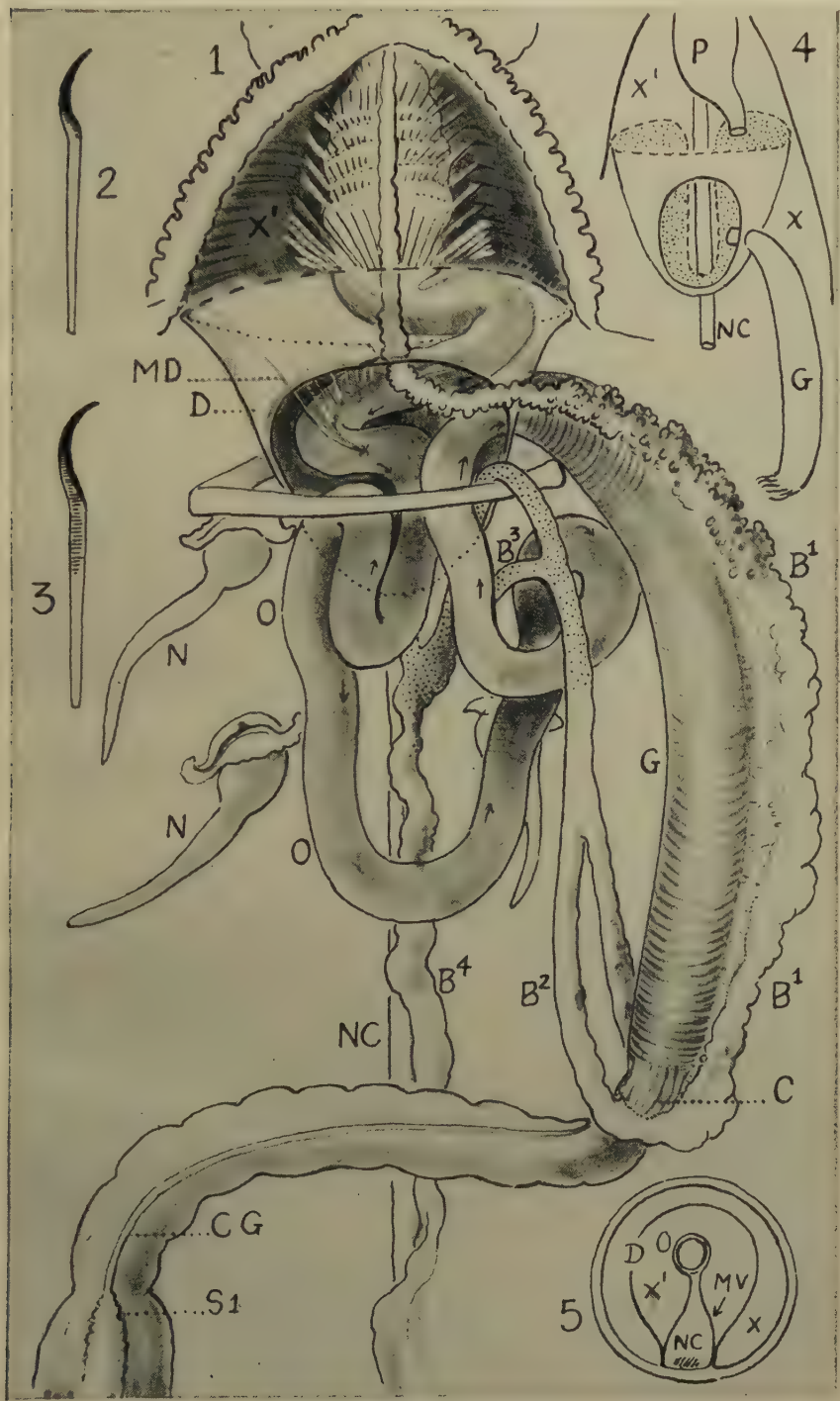

ECHIURUS ECHIURUS ALASKANUS, NEW SUBSPECIES

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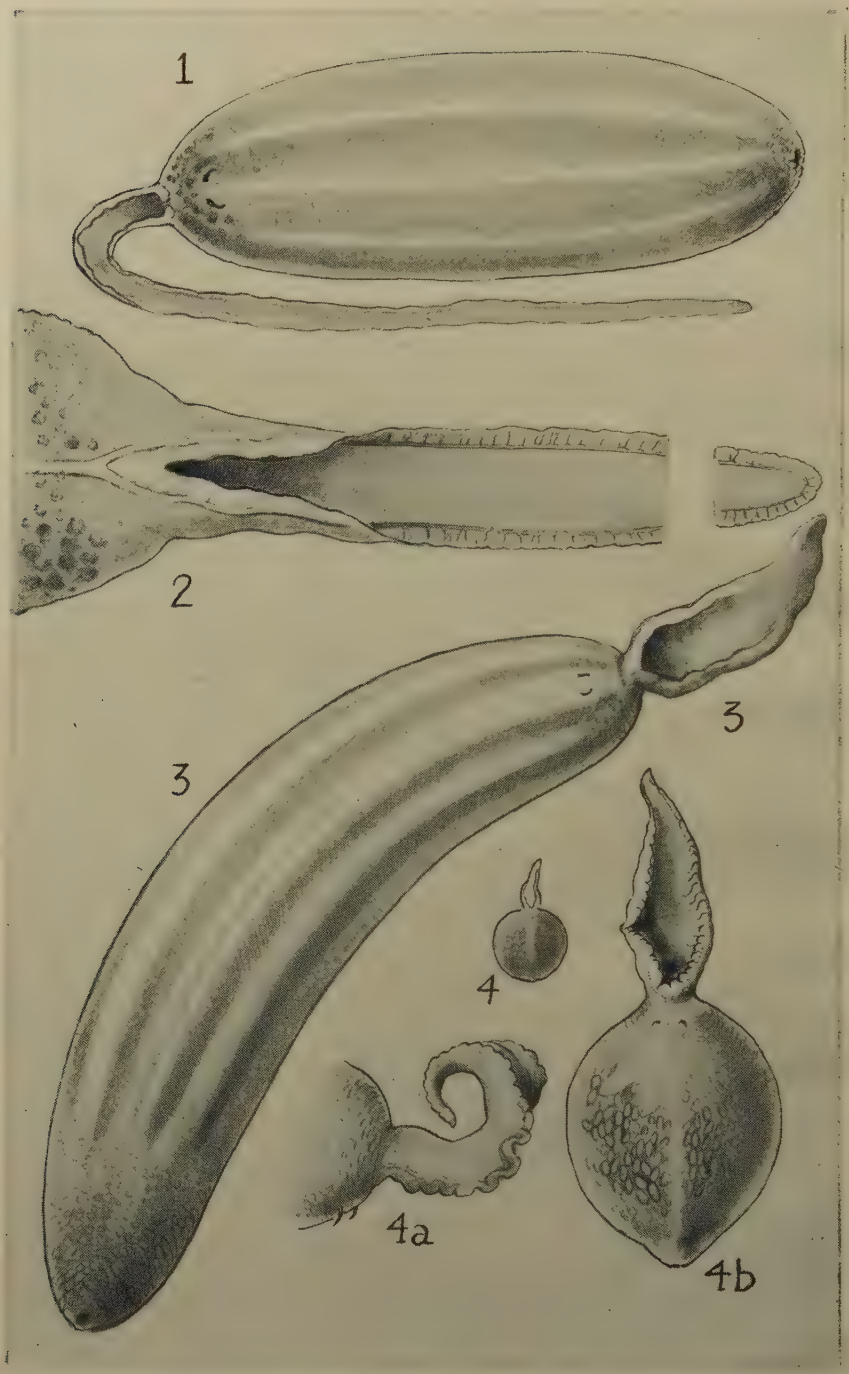

LISTRIOLOBUS PELODES, NEW SPECIES, AND OCHETOSTOMA OCTOMYOTUM, NEW SPECIES

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LISTRIOLOBUS PELODES, NEW SPECIES

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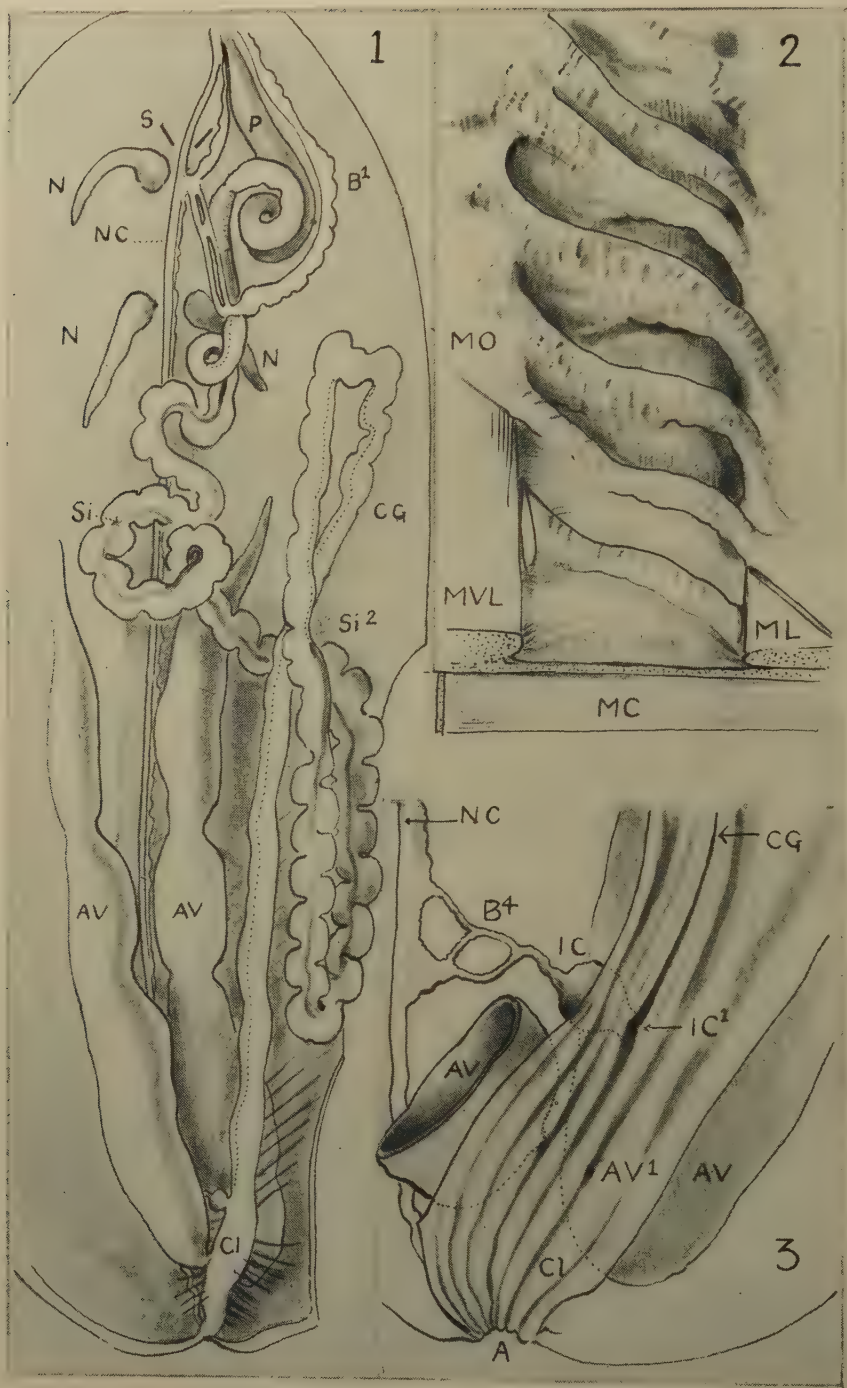

OCHETOSTOMA OCTOMYOTUM, NEW SPECIES

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OCHETOSTOMA OCTOMYOTUM, NEW SPECIES

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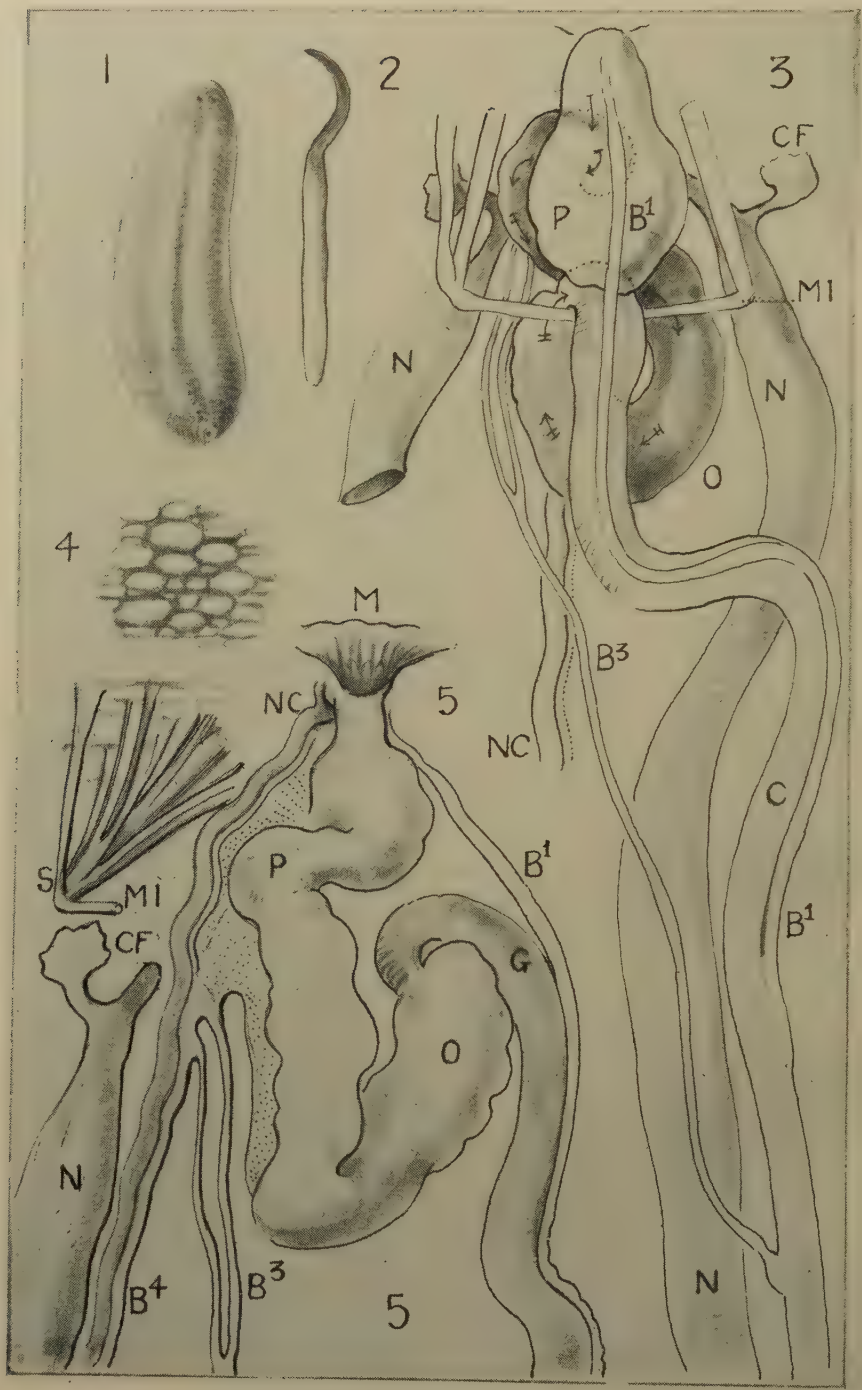

ARHYNCHITE INAMOENUS, NEW SPECIES

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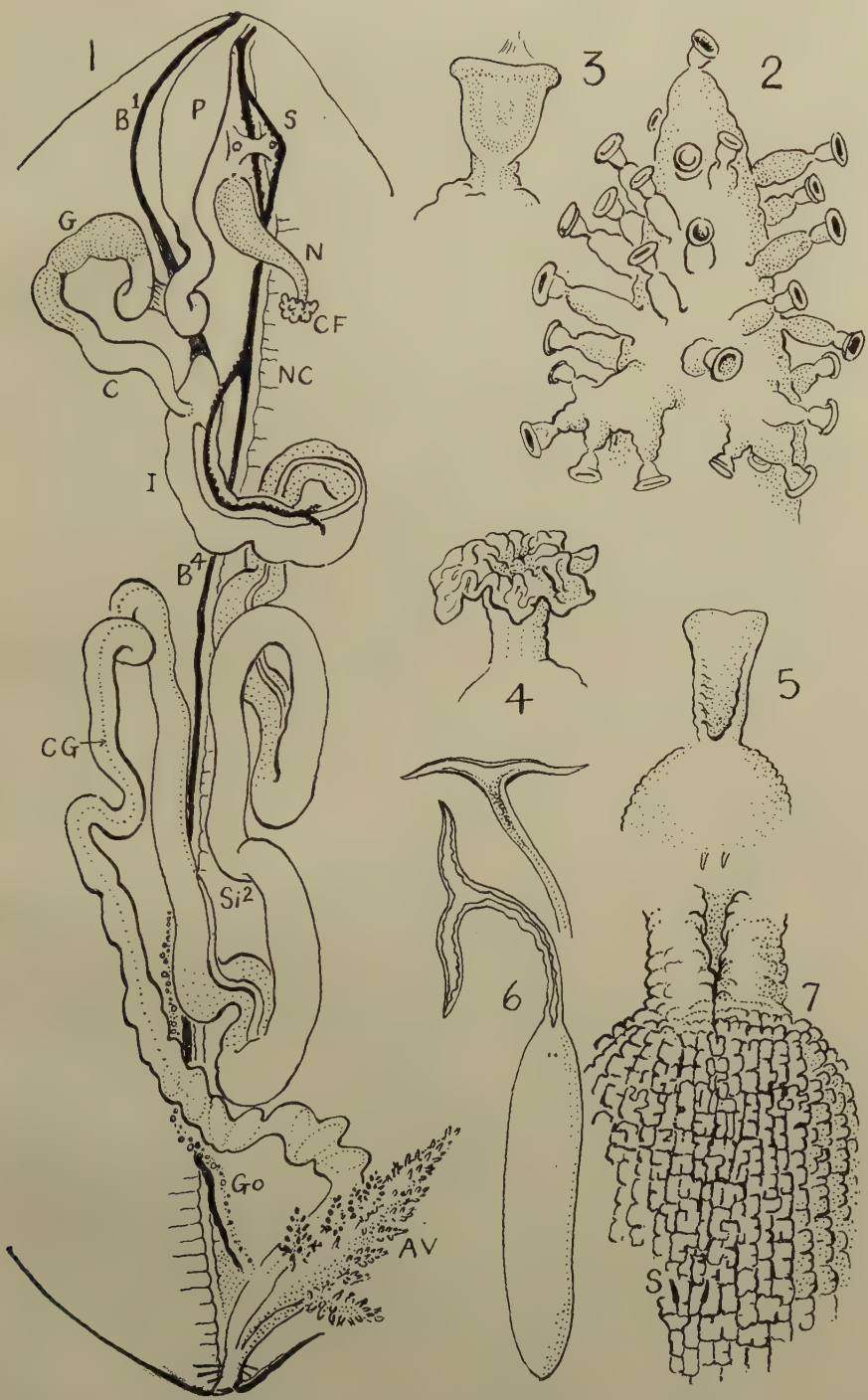

BONELLIOPSIS ALASKANA, NEW GENUS AND SPECIES

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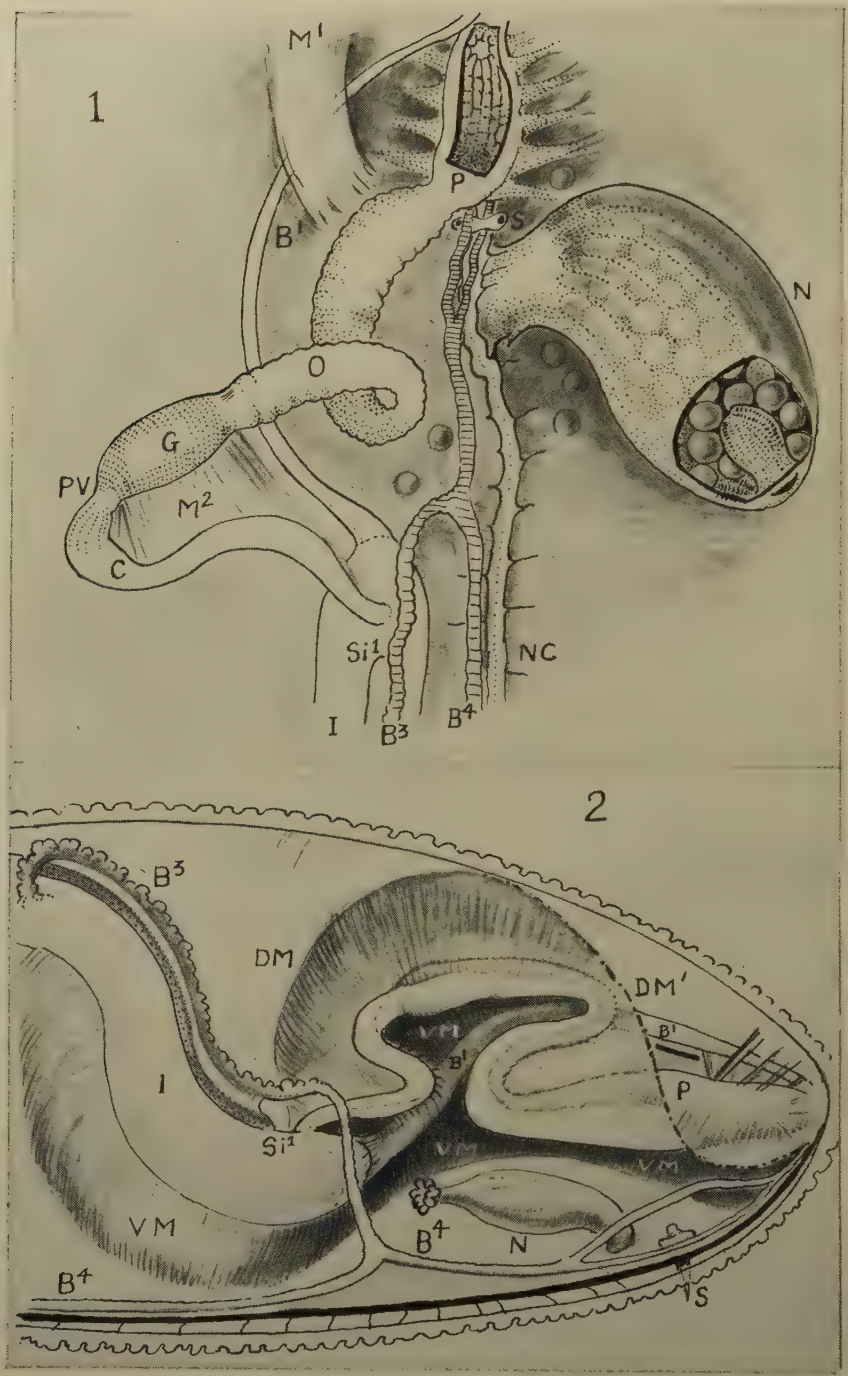

BONELLIOPSIS ALASKANA, NEW GENUS AND SPECIES

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EUBONELLIA VALIDA, NEW GENUS AND SPECIES

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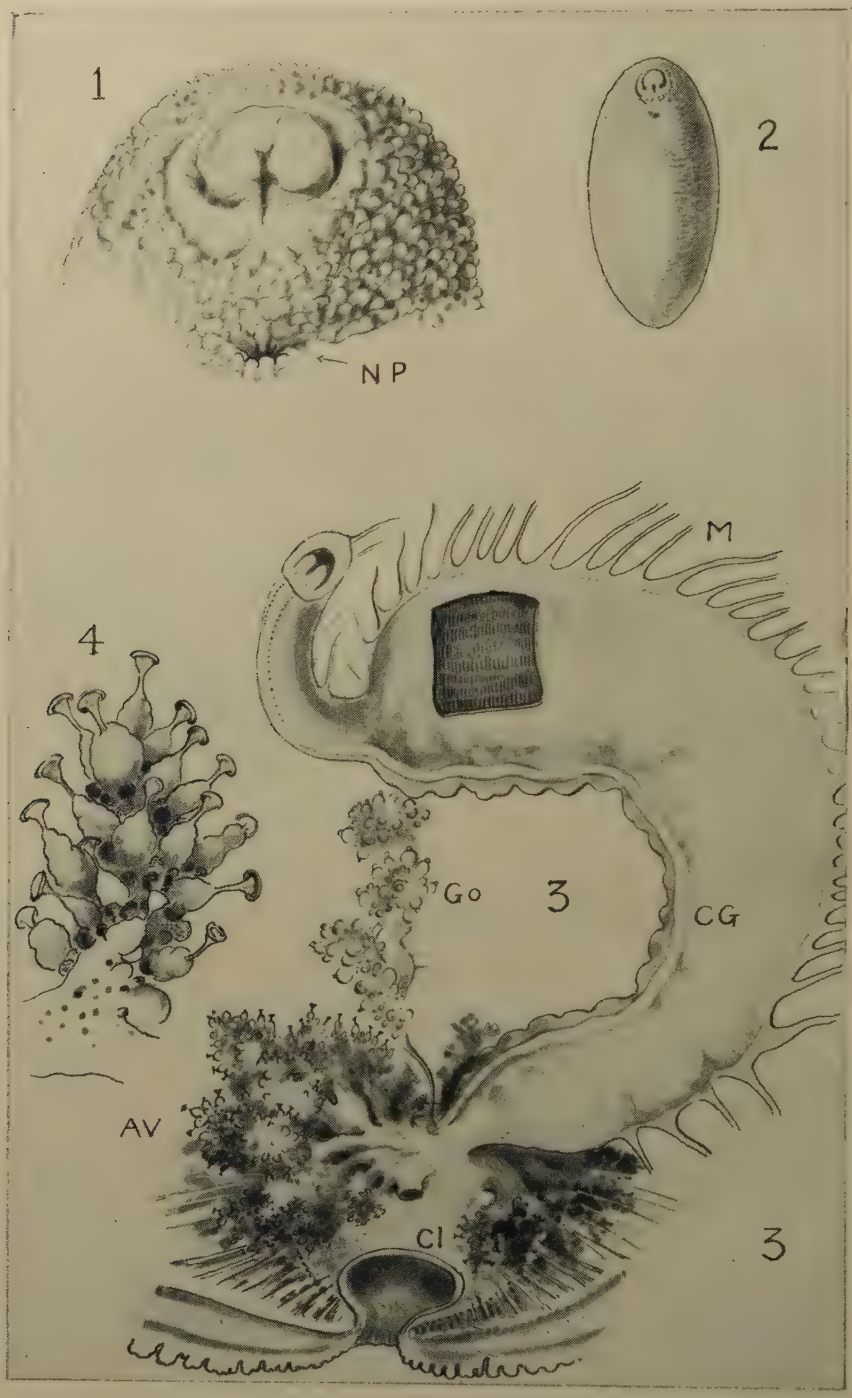

NELLOBIA EUSOMA, NEW GENUS AND SPECIES

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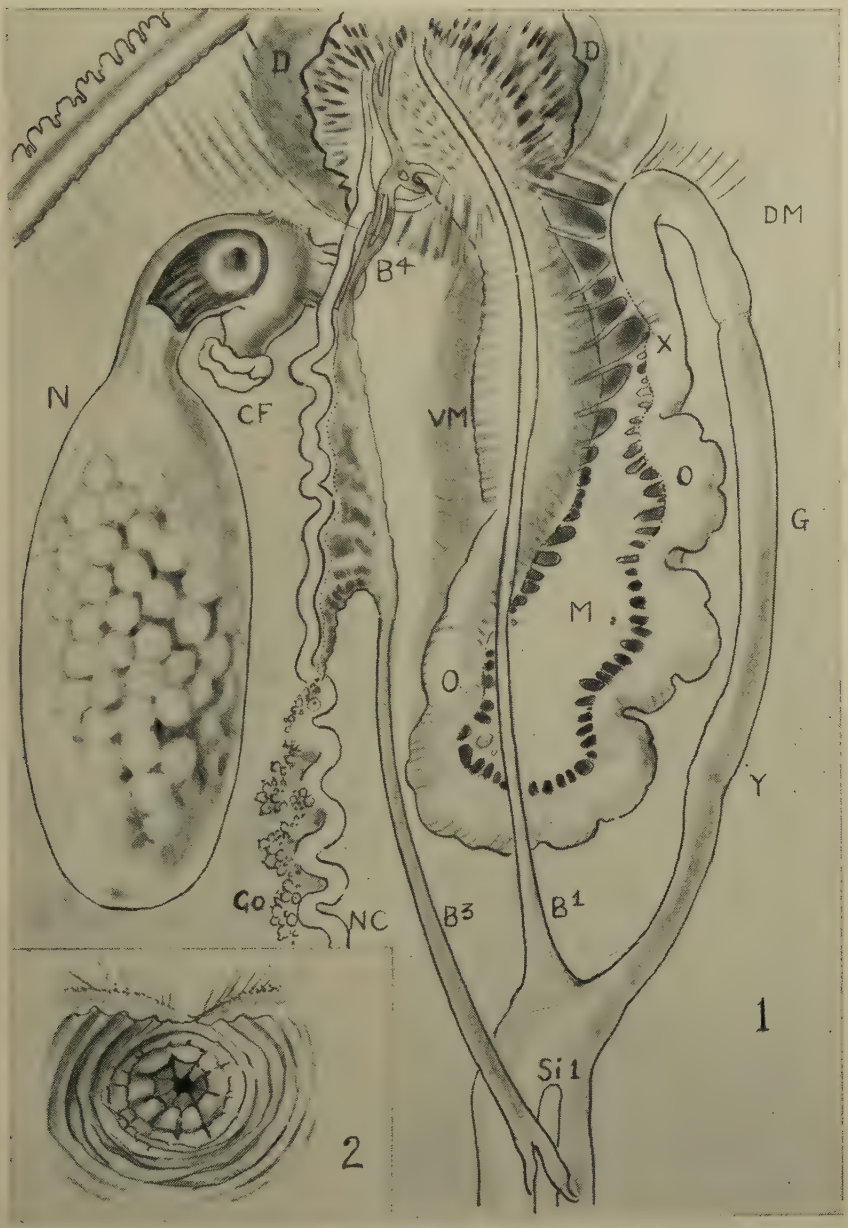

NELLOBIA EUSOMA, NEW GENUS AND SPECIES

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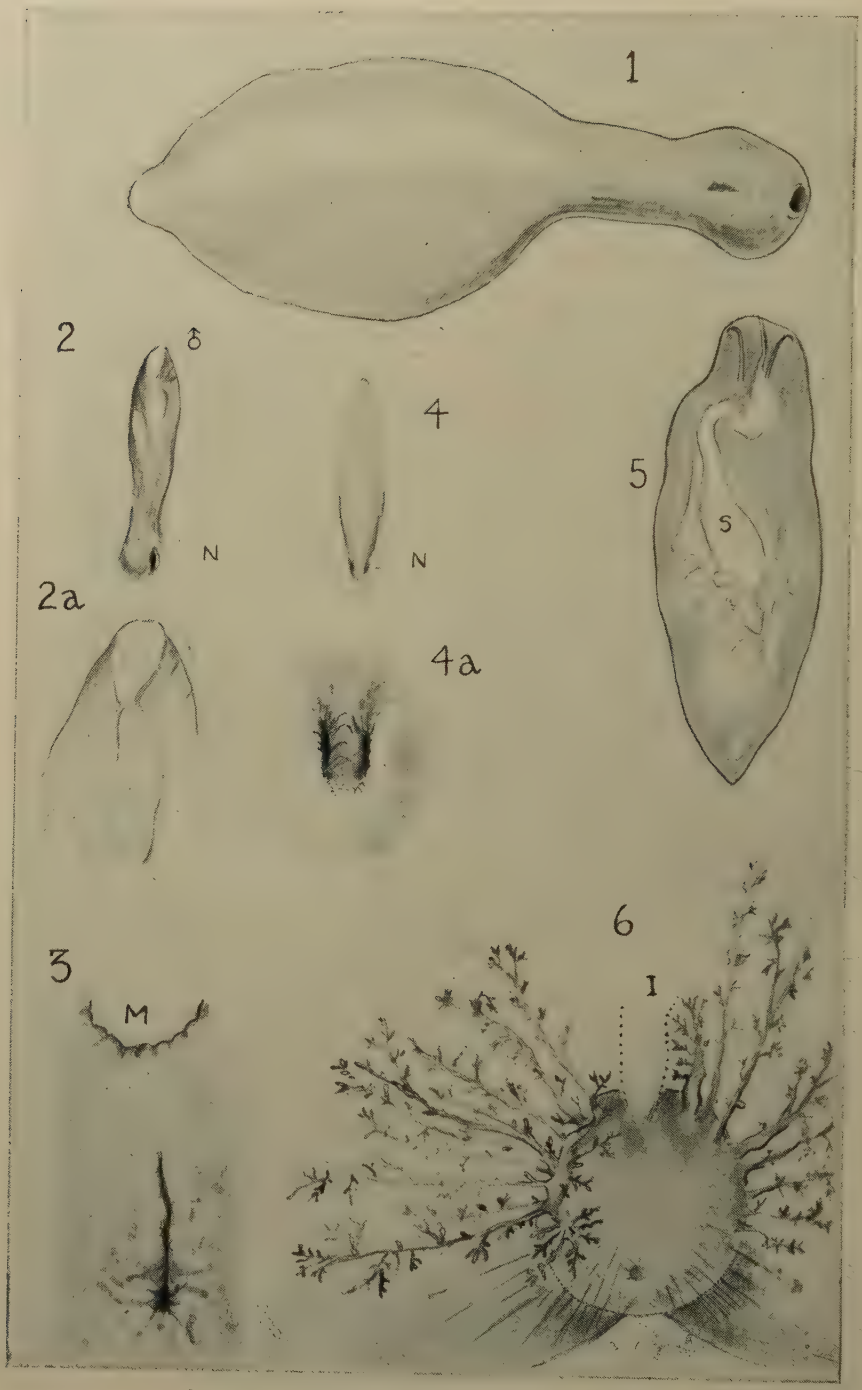

ACANTHOHAMINGIA PARADOLA, NEW SPECIES

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ACANTHOHAMINIGIA PARADOLA, NEW SPECIES

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URECHIS CAUPO FISHER AND MACGINITIE

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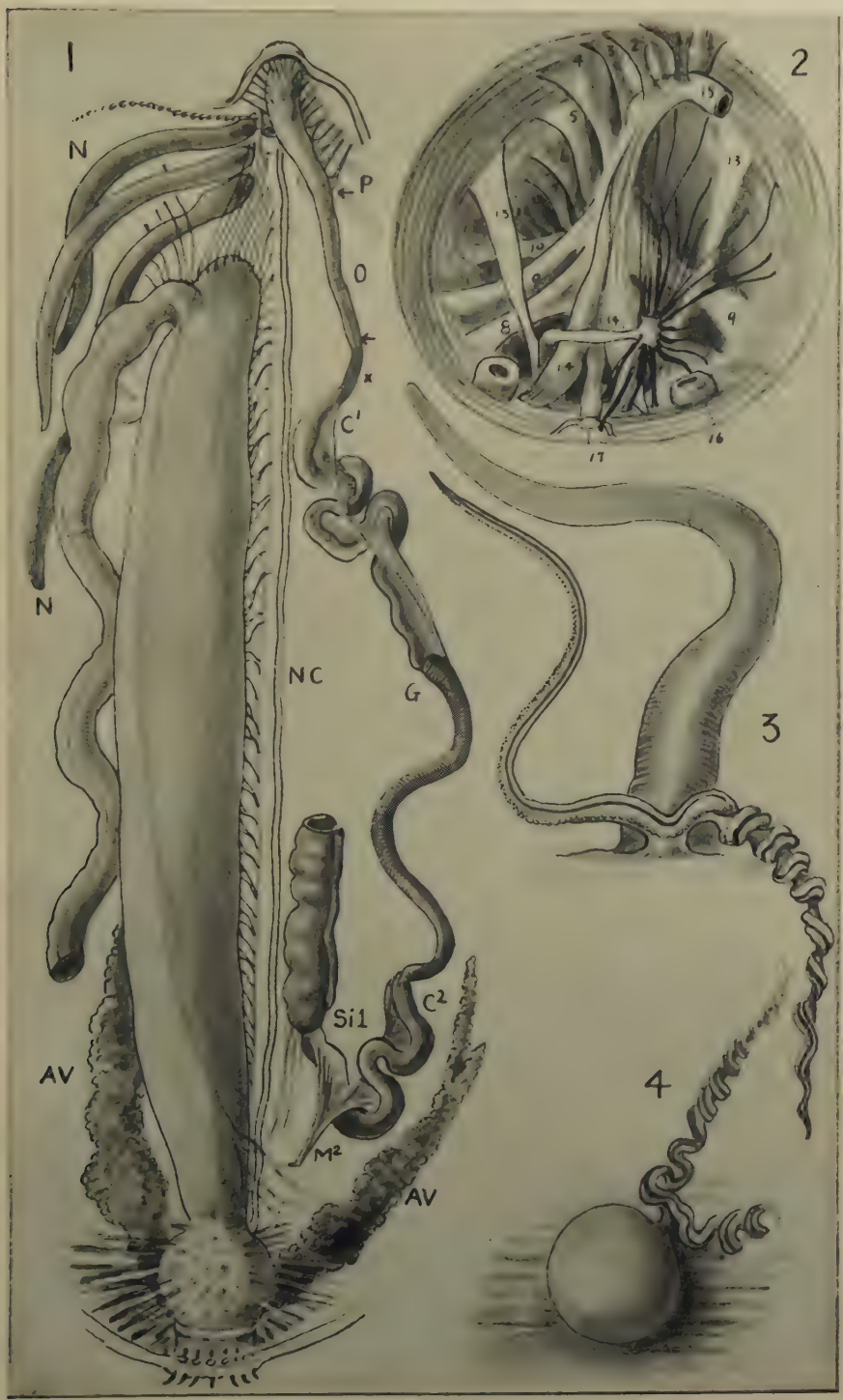

URECHIS CAUPO FISHER AND MACGINITIE

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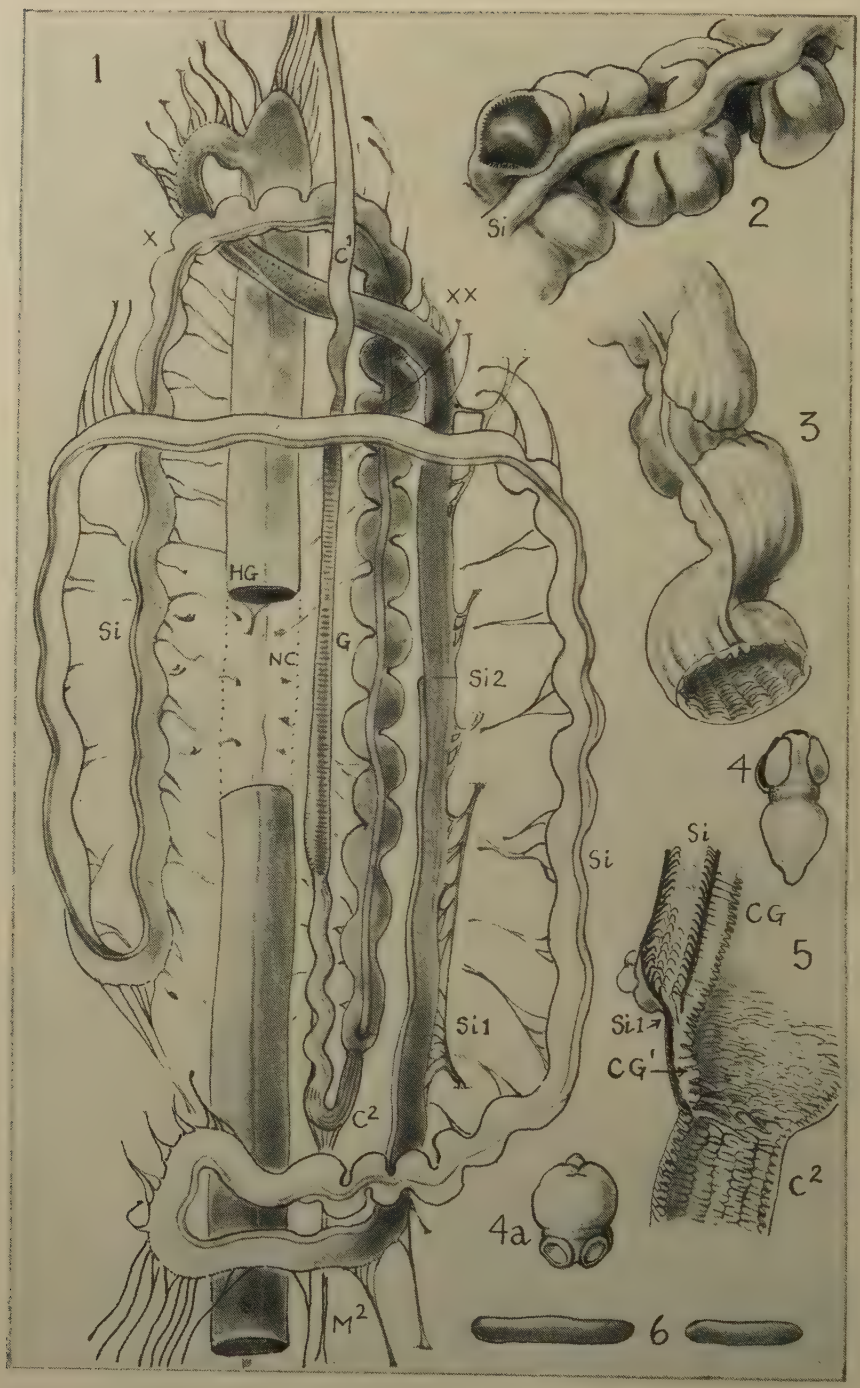

URECHIS CAUPO FISHER AND MACGINITIE

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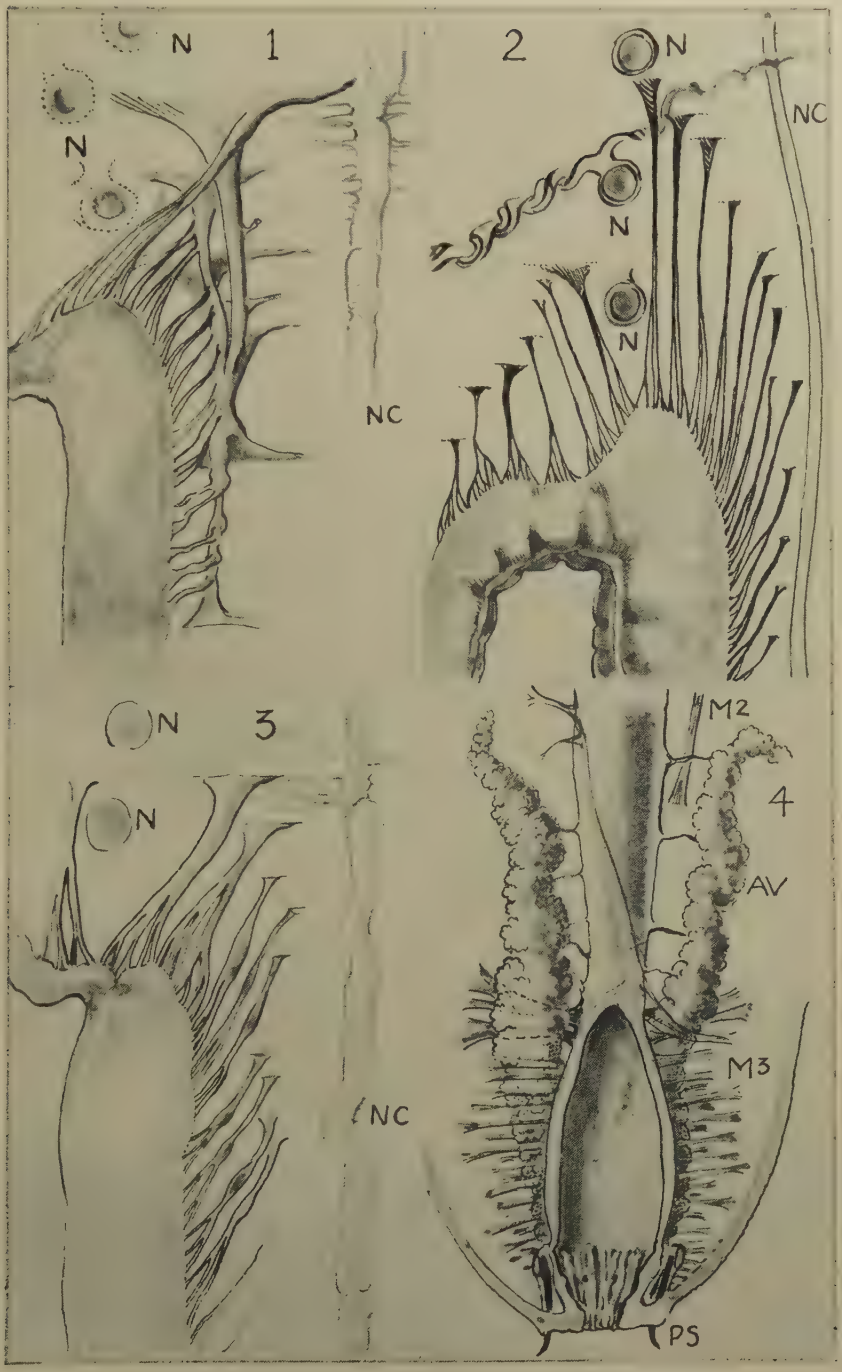

URECHIS CAUPO, U. CHILENSIS, AND U. UNICINCTUS

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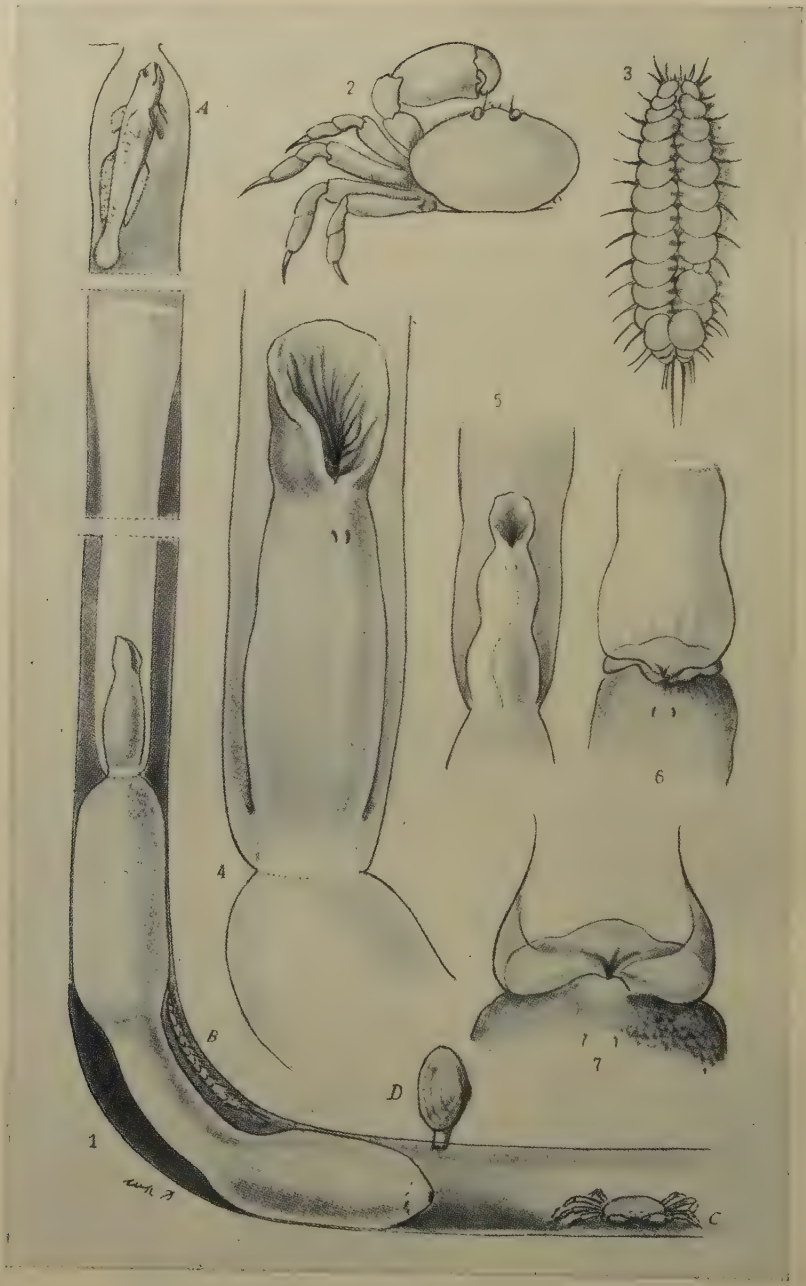

URECHIS CAUPO AND COMMENSALS

FOR EXPLANATION SEE PAGES 291–292